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EDITORIAL COMMITTEE

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JOHN THEODORE BUCHHOLZ
FRED WILBUR TANNER
CHARLES ZELENY

EXPERIMENTAL STUDIES ON
ECHINOSTOMA REVOLUTUM (FROELICH)
A FLUKE FROM BIRDS AND MAMMALS

WITH THREE PLATES

BY
PAUL CHESTER BEAVER

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
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INTRODUCTION

Studies on larval trematodes and life history researches have progressed rapidly during the last few years and it should now be possible to take advantage of the accumulated facts in investigations of less familiar related problems, particularly the still very perplexing problems regarding the reproductive processes of the larval stages. In connection with studies on another species a rough idea regarding the life history of an echinostome species was obtained, and it was my original plan to study some of the less familiar phenomena including the reproductive processes within the snail host. There is at present much disagreement as to the general type or types of reproduction in these stages; parthenogenesis, polyembryony, and various other types of asexual and sexual reproduction each being proposed by various authors. Where studies have been made with special attention to reproductive phenomena the method of approach has been entirely cytological and the results contradictory. It was thought that an analysis of the variation in pedigreed offspring might serve as a favorable approach, and it appeared that the crown of spines and the cuticular spination of an echinostome would provide ideal material for a study of variation if the worms could be cultured in large numbers; and since certain laboratory animals were easily infected, an investigation of the above problems was attempted.

In order to take advantage of the researches already completed a final determination of the species was soon attempted. This proved to be a very considerable problem in itself, however, for so much contradiction and confusion was found that it was not until after most of the studies were completed that a final decision was reached regarding the species studied. Long and tedious studies were necessary in order to elucidate certain points regarding even the morphology of the very common adult worm. Most of my earlier experiments were designed to discover suitable methods for culturing each of the stages in the life cycle and a number of hosts were used with more or less success. It was noticed that the worms from some hosts differed slightly from those of others and two more problems were added by this observation. It was necessary first to prove absolutely that only one species of parasite was being studied, and secondly to determine the amount and nature of the variation due to the type of host. During the experimentation to exclude the possibility of mixed infections certain immunity phenomena were encountered. Only a very preliminary sort of study of these phenomena was possible, but some of the data obtained are interesting enough to report.

The whole of the present report is in many respects only preliminary. The volume of data that had accumulated seemed to require analysis, however, before further studies were made.

Special methods employed are described in the various sections where the reader is most likely to be interested in them. Brief introductions and discussions are also added to the various sections where they are most pertinent. Some repetition is held to be preferred to profuse cross reference and is therefore allowed for clarity.

LIFE HISTORY AND MORPHOLOGY

HISTORICAL

It is probable that the first experimental work on the life history of *Echinostoma revolutum* was done by Pagenstecher in 1857. Although he did not give a description of the encysted metacercaria or give sufficient data on the morphology of the adult to exclude the possibility of misdetermination, it seems fairly certain that he was working with *Echinostoma revolutum* (*D. echinatum*). At any rate his was the first demonstration of the so-called life history of an echinostome. He found that echinostome cysts which were present in great numbers in *Paludina* sp. when fed to young ducks would develop into an echinostome species which he identified as *Distoma echinatum*. He also found cysts in *Lymnaea stagnalis* and *Planorbis corneus* which he considered identical with those from *Paludina*. Some of the other important observations which he made are that unhealthy or starved ducks do not hold their parasites and that the worms mature in about two weeks. He noticed too that although several thousands of cysts were fed to the hosts only about a hundred mature worms could be recovered from them. The gradual depopulation of the gut was explained on the basis of two factors: first, as the worms become mature the suckers become proportionally smaller and are thus less able to overcome the natural flushing of the gut, and secondly, the crown spines are gradually broken off until they are so reduced that the worms are crippled and eventually passed out. The latter is of minor importance if indeed it is a factor at all.

It has been observed many times that the cephalic or crown spines are lost under certain conditions such as rough treatment after poor fixation or death within the host so that fixation cannot be good, but it has not been demonstrated that these spines are shed by a living animal. Johnson (1920) reported that the cercariae have 43 spines while the adult has only 37, and stated that he believed this to be due to a natural shedding. A suggestion from Tubangui (1932b) to which I subscribe is that Johnson observed the spination of another species of cercaria (see page 15).

Ercolani (1881, 1882) reported experiments on this species but his identification was incorrect and his work of no importance here excepting that it has caused incorrect records to appear repeatedly in the literature. This work in which he reported experimental infection in ducks and mice and that of Generali (1881) in which he reported the same species from the duodenum of the dog were accepted by Railliet (1895) and Ercolani's figures were copied into his "Traite de Zoologie Medicale et Agricole." These figures with summaries of Ercolani's experiments have since appeared in English (Neumann-Macqueen, 1905), and thus have been fairly well distributed in Italian, French, German and English literature. This, of course, has a rather important bearing upon the present study because of the uncertainty attached to each of the reports of host and distribution records that might be based upon this or similar work. Wedl (1857) reported, described, and figured a species which he incorrectly identified as *D. echinatum*. Perhaps it was Wedl's description and figure that Ercolani used in identifying his material. They are somewhat similar.

Johnson (1920) was the first to make observations on all or nearly all stages in the life cycle of an echinostome. He was supposedly working on *Echinostoma revolutum*. Whether or not this is true some of his observations are of interest here, for he again demonstrated the method of infection and described some of the developmental stages. He took forty-five eggs from adult worms which he found in a duck, *Marila marila*, and when the miracidia hatched (in about three weeks) he exposed laboratory raised *Physa occidentalis* to them. He learned by subsequent studies that the miracidia develop directly into mother rediae, which after about three months produce a generation of daughter rediae, and these in turn produce the cercariae. As only forty-five eggs were collected it was not possible to infect many snails and consequently the studies on laboratory infections were not extensive. The morphology of the rediae and cercariae was studied on material collected in the field. Metacercariae were found encysted in *Physa occidentalis*, *Lymnaca traski*, and planarians, but he (Johnson, 1920) was unsuccessful in an attempt to recover them from laboratory exposed tadpoles of *Hyla regilla* Baird and Girard and *Notophthalmus torosus* (Rathke). By feeding metacercariae in *Physa occidentalis* he produced an infection in mongrel ducklings from which he recovered eight "full grown" and sixty-five less mature adult worms.

Vevers (1923) fed a young duck some cysts of a form which he identified as *Cercaria echinata* and after 12 days recovered fifteen immature specimens of *Echinostoma revolutum*. In the same year Miki (1923) found the tadpoles of *Rana esculenta* heavily infected with echinostome cysts and upon feeding these to rats and mice recovered worms identified

as *E. cinetorchis* (— *E. revolutum*). The following year Lutz (1924) reported studies on this species. He obtained two infections in the duck (*Cairina moschata*) by feeding it *Physa rivalis* which carried a laboratory infection of metacercariae. The cercariae also came from *Physa rivalis*. More recently Tubangui (1932b) reported observations on both the larval stages and adult worms from experimentally infected pigeons; and Fallis (1934) has infected goslings by feeding them infected tadpoles.

The various stages in the life cycle can now be fairly well described and many of the details regarding the general biology of the species summarized from the researches of others. The present studies were made primarily as a basis for irrevocable identification, and the successful culturing of cercariae and adult worms. For that reason the observations were more or less confined to these stages. They will be discussed in the following order: miracidium, mother-redia, daughter-redia, metacercariae (agamodistome), and adult. The egg is considered a character of the adult worm.

LARVAL STAGES

Miracidium

Eggs collected in feces, washed, and allowed to stand at room temperature hatch in from 18 days to one month. Active miracidia may be seen within the egg much earlier, however, as the flame cells and cilia appear several days before the embryo assumes the elongate shape of the fully developed individual. At about 6 days the young miracidium is nearly spherical, is ciliated, and has two flame cells in the center of the body. In diameter it is about one-half the length of the egg. During the next few days it elongates, dark granules appear in the region where eye spots are to be formed, cuticular plates become evident, and the right flame cell becomes more anterior in position. After 10 or 12 days eye spots are clearly defined, the body is as long as or slightly longer than the egg, and it has, with the exception of size, the appearance of the hatched miracidium (Fig. 11).

The following description of the fully developed miracidium is based on individuals incubated from numerous hosts and from several stocks. Very little variation was observed in the characters described. By inverting a glass funnel in a beaker containing the washed feces, miracidia were concentrated in the neck of the funnel and studied much the same as one would study an infusion of protozoa. As soon as the miracidia hatch they swim upwards, thus collecting in the narrow neck at the surface. *Intra-vitam* stains were found to be useful in differentiating some structures, and others were more clearly shown in stained permanent mounts. Many of the larvae were studied while still within the egg.

More often than not the larva is facing the operculum of the egg. The body is longer than the egg but much less in diameter. This necessitates a flexure which is at the posterior end and is in most cases dorsal, leaving the entire ventral side in contact with the shell (Fig. 11). The space not occupied by the larva is filled with two or three large clear globules which appear to be attached to the miracidium between the first and second row of plates.

The body is covered with large unicellular ciliated plates arranged in alternate fashion in four circumferential rows (Figs. 7, 11). The cilia are nearly uniform in length ($10\text{--}14\ \mu$) over the entire body. The four rows contain, respectively, from anterior to posterior 6, 6, 4, and 2 plates. When stains are used a large elongate nucleus is clearly seen along the posterior border of each plate.

The eye spots are clearly defined as dark crescents along the mesial edge of the lobes of the brain. A few scattered granules are also sometimes present along the posterior border. There is one flame cell in the anterior part of the body at the level of the second row of the cuticular plates, and a posterior one at the level of the third row. The anterior one is on the right side and ventral, the posterior one left and dorsal. The somewhat coiled excretory ducts lead independently to the lateral excretory pores at the triple junction of the posterior plates and those just anterior to them. The "germ balls" lie loose in the posterior two-thirds of the body and are variable in arrangement and number. Between the proboscis or protrusible papilla and the eye spots is a sac-like structure which in other species has been called an intestine. Lateral and ventral to this structure are masses of cells which by their staining reaction seem to be glandular.

The only echinostome miracidium sufficiently described to allow comparison is that of *Echinoparyphium recurvatum* which was recently described by Rasín (1933). Both forms have the 6-6-4-2 arrangement of the cuticular plates, two flame cells whose ducts empty between the third and last rows of plates, eye spots in similar position, and, in general, a very striking similarity is apparent. There is, however, one difference according to the descriptions given. In *E. revolutum* the posterior plates appear to be dorsal and ventral while in *Echinop. recurvatum* they are lateral, one on either side of the body.

After hatching, the miracidia swim rapidly and almost constantly until they find a host or finally die. Eighteen hours is the longest free-swimming period observed but under natural conditions it may be somewhat longer. The exact method of penetration was not determined, but they were often observed spinning vigorously with the proboscis-like anterior end undergoing a rapid succession of expulsions and withdrawals

while in contact with the body of the snail. None of the individuals observed were successful in breaking through.

Upon entering the snail, which may be almost any pulmonate, the miracidia metamorphose either directly into a mother-redia or into a sporocyst. Johnson (1920) believes that the sporocyst stage is omitted, but Rasin's studies on the closely related species *Echinop. recurvatum* and Mathias' (1925) observations upon *Hypoderaeum conoideum* indicate that the sporocyst does occur.

In the present study sporocysts were not observed, but no special effort was made to discover them. Snails were infected by the following method: the feces from infected hosts were washed repeatedly by decantation and the coarse material strained out, thus concentrating the eggs and minimizing the bacterial growth. The sediment containing the eggs was incubated at room temperature in 500 cc beakers or similar containers, and the water changed as often as was necessary to maintain freshness. As the miracidia began to hatch they came to the surface where they could be seen by looking through the glass container at right angles to a beam of light. When it was known that miracidia were present in the culture a few snails were placed in a coarse screen cage and partially immersed for a day or two.

Thus far this method has not been as successful as is desirable. Either because of improper conditions after exposure or because of too heavy infections, practically all the snails died before mature cercariae were produced. In the first of these experiments 96 snails were exposed and only 3 lived to produce cercariae; 3 others lived to the end of the experiment but were uninfected. As the snails died or were observed to be dying they were opened and examined for developmental stages. Only rediae were found in snails opened in less than six weeks after exposure, and mature cercariae did not develop until the ninth or tenth week. The snails were kept in a basement aquarium where the temperature ranged between 50 and 60° F, and were fed regularly on lettuce. Later attempts to infect snails were equally unsuccessful. Each snail was exposed to only 3 or 4 miracidia and kept in a green-house aquarium where the temperature was 80-110° F. Fewer snails died but none that lived were ever found infected.

Redia

The rediae of *E. revolutum* are so variable in size and shape that description of them is difficult. For that reason and for the reason that there is a very close similarity between all of the species of the genus none of the descriptions made thus far differentiate it from that of closely related species. My own observations have not been detailed enough to

describe this stage adequately even when added to and compared with other descriptions. Johnson's description (1920) of it is rather detailed but must be accepted with the reservation that it was made from studies on questionable material.

In one instance mother-rediae were observed in a snail that had been exposed to miracidia 62 days previously. These mother-rediae are large and elongate, measuring about 2 mm in length and 0.3 mm in width when extended. The pharynx is about 0.1 mm in diameter, which is relatively larger than that of the largest daughter-rediae. The collar, which in the daughter-rediae is fairly conspicuous, especially in the younger ones, is barely distinguishable in the old mother-rediae and likewise the posterior projections are not pronounced. Eighteen posterior and 9 anterior flame cells were observed.

The very young daughter-rediae are colorless but gradually accumulate an orange-colored pigment as they become older, so that the largest ones are always somewhat colored. This seems to be characteristic of all echinostome rediae. The pharynx and gut change in relative size as the rediae increase in total length. In small individuals they appear very large, and in the largest ones very small and inconspicuous. For example, a specimen which measures 0.28 mm in length has a pharynx which is $35\ \mu$ wide and in one 0.85 mm long it is $40\ \mu$ in diameter. Both specimens are about equally extended. In these same specimens the gut measures respectively 0.15 and 0.30 mm in length. A birth pore which seems to be dorsal can be seen on some specimens, and a collar is evident on all contracted ones. The pigment makes flame cell studies in the larger ones difficult, and in the smaller ones the flame cells are themselves so small that they are difficult to study. Although 36 flame cells were not seen in any one specimen it seems probable that there are four groups of them, 2 posterior ones near the lateral projections and 2 about half-way to the anterior end near the distal end of the gut, and that each of these groups contains 9 flame cells. Johnson (1920) described them in two groups, 17 in the anterior and 18 in the posterior.

Cercaria

The cercariae of the genus *Echinostoma* exhibit but few specific characters by which they may be distinguished. Tubangui (1932b) in working with the two species *Echinostoma revolutum* and *Euparyphium* (*Echinostoma*?) *murinum*, found that he could not distinguish one from the other except by counting the spines on the cephalic crown. In some forms it is difficult to study the cephalic spination, and accuracy in any case is not easy to attain. It naturally follows that any of the earlier descriptions which omitted the accurate notation of number and distribu-

tion of the spines must be considered as doubtful species save where other circumstances such as feeding experiments confirm the identifications.

The several researches on the life histories of echinostome species have demonstrated a relatively wide range of hosts for all of them, and the practice of using the host as a diagnostic feature must be abandoned in favor of more detailed morphological descriptions. For purposes of identification there seems to be no morphological feature in the echinostome species as reliable and serviceable as the cephalic spination. Some of the cercariae are alleged to be spineless, but none of these spineless "echinostomes," the "Agilis" group of Sewell (1922, p. 106), have, to my knowledge, been definitely shown to develop spines in later stages. The nature of the cephalic spines is perhaps no more characteristic of the various species than any one of a number of other features, but most of the other characters are either obscure or variable with the conditions under which they are studied. After long and tedious studies on the excretory system and the so-called "flame-cell formula" or "pattern" of this and other species, I am inclined to agree with Wesenberg-Lund (1934, p. 8) that while it is an admirable ambition it is also a practical failure, and I must confess along with him and Tubangui (1932b) that I cannot with absolute certainty determine the number of flame cells in this species. The measurements and figures were for the most part made on fixed specimens, since there is less variability due to methods of fixation than to the amount of pressure exerted on the living specimen. Three different methods were used in studying the spination: (1) living specimens were compressed and stained with the usual *intra-vitam* stains; (2) fixed specimens were cleared in glycerine to which a small amount of methylene blue had been added; (3) fixed specimens were stained in the usual manner and cleared in oil of wintergreen to which a few crystals of picric acid had been added. All of these methods are good but the second and third are best. For studying the cephalic spines I have used the second method more than either of the other two, and the third method is best for studying the cuticular spination.

The living cercariae are active swimmers and good creepers on a smooth surface. With the use of the two suckers they are able to creep fairly rapidly in the measuring-worm fashion, and even on relatively large tadpoles they sometimes find their way into the cloaca in a few minutes. They remain active and infective for 10-12 hours, then sink to the bottom and die after 20-24 hours. The swimming movements seem to be random. Numerous experiments were devised to determine whether they are attracted by any of the secondary intermediate hosts, but no action of this kind was discovered. However, after they have come into contact with the body of the host they immediately begin the creeping

movements which seem to be in the majority of cases in the direction of an entrance. This is particularly true on tadpoles. It was noticed that they very rapidly find their way into the small opening of the cloaca, and after a number of observations under magnification it was found that they usually creep downward and posteriorly until they reach the mid-ventral line of the tail, then turn anteriorly to follow this line into the cloaca. Fig. 5 indicates the usual course followed.

The following measurements were taken on a typical fixed specimen: length of body 0.323 mm, width 0.095 mm; length of tail 0.45 mm; oral sucker 41 by 46 μ ; diameter of acetabulum 58 μ , pharynx 17 by 21 μ . The acetabulum is in the posterior third of the body (Fig. 12). The crown-spines over the head are identical in number and distribution with those of the adult. Although there is less difference in the relative size of the various spines there is a noticeable difference that corresponds with the condition found in the adult worms (cf. Figs. 1, 2, 3, with Fig. 9 and Text-figs. 1-5, p. 24). Riech (1927) found the same condition in *Echinoparyphium aconiatum*. Johnson (1920), on the other hand, reported a greater number in the cercaria, 43 instead of 37, and Iwata (1933, p. 1) implies the opposite in the statement that the head crown usually has 37 spines but that the younger ones have only 35. Figs. 1, 2, and 3 are camera lucida drawings of the crown seen from three views. The important features of this region are that there are 5 spines on the lappets, 6 unalternating lateral spines, and 15 dorsal ones in 2 alternating rows. The spines of the oral row are very slightly smaller than those of the aboral.

The cuticular spines are very inconspicuous, but when the specimens are lightly stained with methylene blue and observed without pressure or stained in picric acid after clearing they are distinctly evident over the whole of the ventral surface and almost all of the dorsal. They are most evident between the two suckers.

The oral sucker and pharynx are joined by a fairly long prepharynx which is rather indistinct. The esophagus and crura are also indistinct in unstained specimens. Associated with the oral sucker is a group of ducts which, as Brown (1926) and Wesenberg-Lund (1934) have already noted for *Cercaria echinata* (?), are outlets to a group of gland cells which are situated lateral to the esophagus (Fig. 12). There are 12 of these ducts, but whether a single gland cell is attached to each could not be determined. These cells and ducts are arranged in two groups. An anterior one in contact with and lateral to the esophagus empties through the three pairs of ducts which pass dorsally over the oral sucker and terminate at its dorsal lip, and a second group is more posterior. The three pairs of ducts from the posterior group are less easily demonstrated,

but by using only a small amount of neutral red they are shown to be more coiled and much smaller. In fact, they do not look exactly like ducts, being somewhat too irregular (Fig. 6). In about half of the toto mounts of the adult worms these larval structures are still noticeable as 6 minute papilla-like structures along the anterior border of the oral sucker (Fig. 9).

The excretory bladder is divided into a small anterior and a larger posterior compartment, both contractile. A single duct runs posteriorly into the tail and bifurcates abruptly into a right and left tributary with an opening (?) to the outside in the region of the 40th-50th circular muscle band, which is about 0.1 mm from the base of the tail. The two main excretory trunks pass anteriorly, lateral and dorsal to the acetabulum, where they enlarge somewhat and are filled with numerous (40-80) refractive granules to about the level of the pharynx. Here they narrow down and as they reach the level of the oral sucker turn back to form a complete loop and extend almost to the posterior end of the body where they again turn anterior and extend to the region of the oral sucker. Fine vibratile patches are numerous in the canal that extends from anterior to posterior and are sometimes confused with flame cells. The total number of flame cells is probably 36 although it is possible that some were not found. The region between the two suckers is opaque and no flame cells were found in that particular portion of the body. The flame cells are arranged in 6 groups of three each, making a formula $2 [(3 + 3) + (3 + 3) + (3 + 3)]$. Fig. 12 shows the distribution of the units found. Sewell (1922) has used the excretory system as one of the characters for separating the echinostome cercariae into the three groups "Echinatoides," "Coronata," and "Echinata." On the basis of Johnson's (1920) description of the cercaria of *Echinostoma revolutum* he placed it in the "Coronata" instead of the "Echinata" group, although he had originally put it in the latter and named the group after it. Sewell was correct in making *Cercaria Echinostomi-revoluti* a member of his "Echinata" group, however, for the cercaria on which the present work was done seems to fit this group in all respects excepting the tail. The presence of a tail fin is one of the diagnostic characters of the "Echinatoides," but Sewell does not definitely state that this character excludes a form from the "Echinata" group. The tail of the cercaria of *E. revolutum* has a distinct fin membrane, but as it is dorsal and vertical it is not seen in all preparations. At the tip of the tail the circular muscle bands do not continue further than the tail fin membrane, which leaves the tip proportionately more delicate than the rest of the tail (Figs. 4, 8, 10).

DISCUSSION.—It is impossible to say how many times this species of cercaria has been described or how many times other species have been

mistaken for it. The original description is accredited to von Siebold (1837). It was not possible to examine von Siebold's description, and many of the older descriptions have not been studied for the reason they are too incomplete to be of use in this work.

In addition to the descriptions of the cercaria of *E. revolutum* by Johnson (1920), Tsuchimochi (1924), and Tubangui (1932b), there are in the newer literature descriptions of eleven 37-spined cercariae. Some of these are readily distinguished from *Cercaria Echinostomi-revoluti* by the character of the cephalic spines and the absence of a tail fin membrane, but the others do not allow a satisfactory systematic treatment. Lühe (1909), Brown (1926), and Wesenberg-Lund (1934) have described *Cercaria echinata*, which is generally accepted as the larva of *Echinostoma revolutum*, as having no tail fin membrane, and as having four corner spines larger than all the other cephalic spines. These descriptions agree throughout with the cercaria of *Echinoparyphium aconiatum* Dietz as described by Riech (1927) and Dubois (1928). While it is not certain that they are all identical, it is certain that they cannot be distinguished from each other and are all very different from the cercaria of *Echinostoma revolutum*. *Cercaria limbifera* Seifert, 1926, as originally described has 37 spines but differs from the cercaria of *E. revolutum* in size, arrangement of the spines, and character of the tail. According to the measurements given, it is a much larger form. The tail has both a dorsal and a ventral fin fold, and the 6 lateral spines of the collar are illustrated as being placed in two alternating rows continuous with the dorsal ones, making the arrangement entirely different from that of the cercaria of *E. revolutum*. The redia of Seifert's form has a much longer gut than the average mature redia of this species. Brown (1931) described a form which he considered identical with Seifert's *C. limbifera*. There is at least one very important contradiction in the observations of the two researchers, however. Brown's cercaria has only 35 spines, and the lateral ones are unalternating, as they are in the cercaria of *E. revolutum*. Since they both have the peculiar tail fin over the posterior two-thirds of the tail, both are larger than any of the others, and the rediae are both of the long-gut type, it is probable that Brown has corrected Seifert's observations regarding the number and arrangement of the cephalic spines. Rees (1931, Text-fig. a) who experimented with *C. limbifera* has given the best illustration of its tail. Dubois (1928) described 12 new species of larval echinostomes from Neuchâtel, and four of them are very similar to the cercaria of *E. revolutum*. One of them is identical with it and the other three may also be. All four of these cercariae are 37-spined forms with the spination formula $(5) + 13 + 1 + 13 + (5)$, according to Dubois's method of writing it. No figures of them are given, and the descriptions of the spines are much too

brief to be of use in separating the 4 species. The description of *C. helvetica* xxiv agrees throughout with the cercaria of *E. revolutum*. The rediae are also identical, and the two are doubtless identical species. The only difference in the two forms *Cercaria helvetica* xxii and xxiii and the cercaria of *E. revolutum* is the absence of a tail fin in the two former. *C. helvetica* xxii is a little larger than *C. helvetica* xxiii, but in other respects they are very similar if not identical. The data given for *C. helvetica* xxv hardly if at all constitute a description. The spination is given as identical with *C. helvetica* xxii, xxiii, and xxiv. A tail fin fold is present, and the gut of the redia reaches almost to the lateral appendages, being much longer than in any of the 3 other forms mentioned above. I am doubtful, however, if the length of the gut in the redia is reliable in separating species of the echinostome cercariae. *Cercaria trivolis* Cort, 1914, was found in the same host from the same general region as the cercaria on which the present study was made (Cort, 1914, 1915). The cephalic spines were not described in detail and the tail fin membrane was not mentioned in the description, making it necessary to examine the type material in order to confirm the suspicion that the two are identical. Very excellent preparations were made available to me by Professor Henry B. Ward in whose collection the "type" specimens were deposited. A dorsal fin is present in *C. trivolis*, and the spination as well as all other features are identical with my own specimens.

The relation of *C. Echinostomi-revoluti* (von Siebold, 1837) to the most similar forms may be summarized as follows: *Cercaria echinata* as described by Lühe (1909), Brown (1926), and Wesenberg-Lund (1934) all differ from *C. Echinostomi-revoluti* in cephalic spination, the absence of a dorsal fin on the tail, and the character of the rediae. They are all probably identical with *C. Echinoparyphii-aconiati* as described by Riech (1927) and Dubois (1928). *Cercaria limbifera* Seifert, 1926, differs in the tail fin, which extends along the posterior two-thirds of the tail and is both dorsal and ventral; and it probably has only 35 cephalic spines instead of 37. *Cercaria helvetica* xxii Dubois, 1928, differs from *C. Echinostomi-revoluti* only in the length of the gut in the redia. The cercaria of *Echinost. revolutum* described by Johnson (1920) is a 43-spined form that is in all probability a misdetermination. *Cercaria trivolis* Cort, 1914, and *Cercaria helvetica* xxiv Dubois, 1928, are synonyms of *Cercaria echinostomi-revoluti* (von Siebold, 1837).

ADULT

Morphology and Size Variation

Three hundred stained permanent mounts are used as a basis for this description. The worms vary from 0.3 to 21.4 mm in length, and,

except for an interval of about 4 mm between the lengths 13 and 17 mm, the specimens used are fairly evenly distributed in size and almost reach the maximum size given in previous descriptions. Leidy (1888) reported specimens up to 25 mm, and Barker and C. A. Beaver (1915) give 22-30 mm as the length for *Echinostoma coalitum*, which is identical with *E. revolutum*.

Echinostoma revolutum becomes mature, that is, it begins producing ova, when it attains a length of 4 to 7 mm, differing considerably in the various hosts. The range then for mature worms is from 4 to 30 mm in length. This size range is so great that a description of any one size is grossly inadequate for an accurate diagnosis of all other sizes, and a description by the ordinary methods is impractical when applied to worms having so great a range in size. This would not be true, however, if it were possible to give proportionate measurements applicable to all sizes which, as is shown below, cannot be done. Practically every feature has been measured and plotted; and in no instance is the proportion between two organs or structures a constant throughout the series.

The worms used were all killed by dropping them from warm tap water into Gilson's fixative heated to 65° C. This method gave fairly uniform results, leaving the worms well extended. Relaxing the worms by shaking was avoided because of the possibility of injury to the cephalic and cuticular spines. For very large worms it was necessary to raise the temperature to 68-70° C in order to get straight specimens. As soon as the specimens straightened out they were pipetted off and the fixation completed in warm solution. No flattened specimens were used, for if worms are even slightly flattened their body proportions are greatly altered.

The greatest width of the body is at the acetabulum in immature specimens, and in the region of the uterus in mature ones. Charts 1, 9, and 10 show the plotted measurements and the partially smoothed curve which expresses the ratio between body length and width. In the smallest specimens the length is three times the width, and it gradually changes to about ten times the width in the largest ones. In worms that have died without fixation the ratio of length to width is often as much as 15:1. In like manner the acetabulum changes from one-fifth to less than one-fifteenth of the body length (Charts 1, 11, and 12).

The position of the acetabulum and ovary is frequently used in describing this and other species. Their position in *E. revolutum* is shown for all sizes up to 20 mm on Charts 4, 13-16. In the smallest individuals the ovary lies within the posterior fifth of the body, but when a length of 5 mm is reached it becomes more anterior and remains near the middle of the body for all larger sizes, being slightly nearer the

anterior end in individuals over 10 mm in length. The distance from the acetabulum to the ovary or that part of the body occupied by the uterus, shifts from about one-fifth of the body length to one-fourth of it, varying considerably on either side of the line, but in no case is it as much as one-third or as small as one-sixth of the length of the body. The preacetabular region becomes less in proportionate length as the animal increases in size. In the smallest individuals, less than 1 mm in length, it is about one-half of the body length, and in the larger ones it is only one-sixth to one-eighth of it.

The relative size of the suckers and the cephalic collar is shown in Charts 2, 3, 17, and 18, where it may be seen that the acetabulum increases in size at a greater rate than does either the oral sucker or collar. The acetabulum and oral sucker are almost equal in the smallest individuals, but in larger worms the latter has a diameter of less than one-third of that of the acetabulum. The diameter of the collar is almost 2 times that of the acetabulum in small individuals and in larger ones it is about equal to it, while in the largest ones the collar is only three-fourths as large as the acetabulum.

The transverse diameter of the pharynx is usually only slightly less than its length. In all sizes of worms above 2 mm it is about equal in length to the diameter of the oral sucker, and in very small worms it is somewhat less, about two-thirds (Charts 19 and 20).

It is difficult to express the size of the testes and ovary because of their variability in shape and the consequent inadequacy of length and width measurements. An expression of the volume of each would of course be ideal but impracticable. The average diameter (half the sum of width and length) is used here as the most practical measurement of size (Chart 5). The posterior testis is slightly larger than the anterior one in most individuals but here the average of the two is used. After sexual maturity is reached the average diameter of the testes is in all sizes of worms about one-twentieth of the total length of the body, and the ovary about one-thirtieth. These proportions, of course, do not hold true for the youngest specimens, and there is a good deal of variability in all sizes.

None of the structures or regions measured and plotted can be described as having a constant proportion to any other part of the body in all sizes of worms, although after maturity is reached some of the ratios are fairly constant. The oral sucker is equal in diameter to the length of the pharynx; the average diameter of the ovary is about one-thirtieth of the body length; the average diameter of the testes is about one-twentieth of the body length; and the ovary is near the middle of the

body. The length of the region between the acetabulum and ovary is also fairly constant after the uterus is formed, regardless of the number of eggs it contains.

BODY SPINES.—In addition to changes in body proportions there are also structural changes caused by the growth and aging of the worms. The cuticular spination is an example of this, as illustrated on Charts 7 and 8. Cuticular spination also varies in the different hosts. In young individuals from all hosts the dorsal spines extend to the region of the acetabulum, and in the very young individuals, less than two days old, the whole of the dorsal side of the body bears minute spines. Ventrally they reach to the posterior end in specimens up to about 3 mm. With increasing age the dorsal rows diminish in number until they have entirely disappeared in some individuals from bird hosts. Ventrally the spination reduces much less in extent; and it also differs in the bird and mammal hosts. The posterior limit of the spines moves forward more slowly in mammals than in birds, sometimes reaching the ovary in bird hosts but rarely going anterior to the anterior testis in those from mammals. Anterior to the acetabulum the number of rows of ventral cuticular spines is apparently not much altered by age or host. Counts made on all sizes of worms vary between 28 and 42 rows from the genital pore to the anterior end, but there seems to be no correlation between high or low counts and the age or size of the worm. The mean is doubtless much nearer the higher number, probably 36-38. The counts cannot be very accurate since some of the posterior rows are usually folded under the acetabulum. The rows on the dorsal and ventral sides are joined laterally, and the spines of successive rows alternate, being arranged in oblique rows as well as transverse.

The size of the cuticular spines cannot be determined very accurately as it is rarely possible to get accurate measurements on both the length and width of the same spine. However, the length of the lateral spines and the width of the dorsal or ventral ones can be measured. Chart 7 gives the length of these spines in the tenth row measured at the lateral margin of the worms. They become progressively smaller in proportion to body length, and in worms from bird hosts they are relatively longer than in those from mammals. The relation of width to length of the spines also changes as the length of the worms increases. The width of the ventral spines plotted against the length of the lateral ones of the same row shows that the width changes from one-half to almost equal the length in large specimens from bird hosts. In those from mammal hosts the ratio of width to length is nearer 1:1.5 in the largest specimens.

A point that should be noted here is that this species is spiny on the ventral side of the body in all individuals, but the larger specimens, 10

mm in length or more, may be without dorsal cuticular spines. Several instances were observed in which the worms were entirely without spines when taken by autopsy that had been delayed so long that the worms were dead for several hours. This condition is not due to a loss of spines alone, however, but to a loss of the entire cuticula. In some cases portions of the cuticula may be seen adhering to the body in small patches. It should be added also that this character, the distribution of the cuticular spines, which has been used as an important character in both specific and generic diagnosis of echinostomes, should be as thoroughly investigated for other species, for just as it cannot be said that *E. revolutum* is either with or without dorsal cuticular spines without reservation, the same probably holds true for other species.

COLLAR SPINES.—Except in cases where spines are lost or duplicated, or where accessory spines appear, there are 37 cephalic spines in all of the several hundreds of specimens examined. In other words, *E. revolutum* is a 37-spined species but does not in all cases bear exactly 37 spines. In well fixed worms the spines are not often lost but are sometimes broken in handling. In fact they are so well attached in the living worm that it is difficult to extract them at all. On the other hand, a worm that has been dead a few hours in the gut of its host easily loses both cephalic spines and cuticula and in some cases may be entirely without either and still appear fairly normal in other respects.

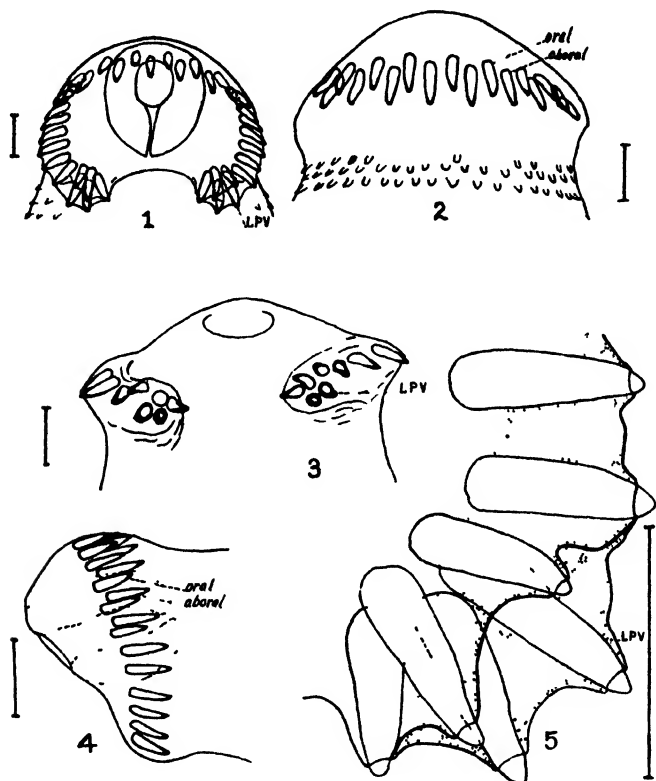
The cephalic spination of 220 worms was observed minutely and the condition of each spine carefully noted. Of this number, 173, or 79 per cent, were found to be entirely normal, i.e., they bear 37 typically placed spines, all of which are normal in size and shape. The other 21 per cent fall into 3 general types of abnormalities. (1) Spines may be missing either because of having been injured in life or improperly handled after fixation. Usually these spines can be counted, however, for a scar is often noticeable and even when a scar cannot be seen the vacant space is evident. Thirty-one of the 220 worms were abnormal in this respect. (2) A less common type is produced by accessory spines, which are most common in the larger individuals, being added where spines normally do not occur. They are smaller than the others in all but one case observed and are easily distinguished from them. In a few instances accessory spines were observed growing from the same position as a normal one, a condition described here as a "duplication." Accessory spines were observed in 17 of the 220 individuals. (3) A third type was observed in 11 of the 220. In these the position of the spines is normal but one or more of them are much smaller, being in some instances very minute. Their size and position suggest that they are being regenerated to take the place of spines that have been lost by injury.

Due to the three types of abnormalities described above, particularly the first, it is important to give special attention to the arrangement of the spines of the collar. Fortunately this character is almost invariable and for that reason is of greater value in diagnosis than spine number or size. Even in specimens that have died in the host and lost most of their spines an accurate determination may often be made if some region including one of the lappets has retained most of the original spination.

Although the grouping of spines for description is somewhat a matter of choice there is a more or less conventional terminology which has been adopted here to facilitate comparison. There are 3 general groups, 2 of which are paired: the 2 corner groups of 5 spines each, 2 lateral groups of 6 each, and a dorsal group containing 15 alternating spines (Text-fig. 1, p. 24). When the specimen is seen in side view or when the lappets are lifted, the position of the lateral and corner spines is seen most clearly (Text-figs. 3, 4). The arrangement of the spines within the various groups may be described as follows: 5 alternating corner spines, 3 of which are on the surface or oral, and 2 that are deeper or aboral; 6 laterals in a single row; and 15 alternating dorsals, 8 of which are anterior or oral to the other 7 which are aboral and continuous with the 6 laterals. The spines are symmetrically arranged; the saggital plane of the animal passes through the median aboral spine.

The relative length of the collar spines to that of the body changes very appreciably as the worm becomes larger (Chart 6). In 1-mm worms the lateral aboral corner spine (*LPV* in Text-figs. 1, 3, 5) varies slightly on either side of 28 μ , in 10-mm ones it is around 90 μ , and in the larger ones it is relatively much shorter, varying 15-20 μ on either side of 120. The relative length of each spine to each of the others usually is not changed by age. In some instances, however, the median dorsal spines become relatively smaller in the older worms, particularly in the oral row in bird hosts. However, in the relative size of the various spines there occurs a good deal of difference which cannot be correlated with age. The lateral aboral one is, in all cases observed, the largest of the 5 corner spines. The median aboral and the middle one of three orals are about equal, the oral one usually being the larger. The lateral oral corner spine is more often than not the smallest one on the collar, and the median oral is about the same size (Text-fig. 5). The most ventral one of the lateral spines is about equal in size to the middle oral corner one or a little smaller than it, and each of the other laterals is slightly larger in a dorsal progression (Text-fig. 4). The dorsal aborals are about equal although the median ones are usually slightly longer than the more lateral ones. The orals are each slightly smaller as a rule than the aboral ones nearest them (Text-figs. 1, 2, 4).

A number of counts and measurements were made on the cephalic spines of the cercaria and metacercaria in order to determine whether spination is the same in both larval and adult stages. There is apparently



TEXT-FIGS 1-5.—Cephalic spines of the adult worm, showing the arrangement and relative size of the individual spines. All are camera lucida drawings. All scales are 100 μ .

1.—Ventral view. Notice that the oral spines of the dorsal side appear to be much shorter than the aborals because they are seen more from end view. Spine *LPV* is the lateral ventral aboral, the largest of the corner spines.

2.—Dorsal view. Aboral and oral spines almost equal in size when seen from the same angle.

3.—Ventral view of specimen killed with the lappets brushed up to show the position of the ventral aboral spines. Corner spines all seen from end view.

4.—Lateral view. Notice that the 6 unalternating lateral spines are continuous with the aboral dorsals. In this specimen the orals are considerably smaller than the aborals.

5.—Ventral view of the corner spines greatly enlarged.

no difference in the number of spines and only a slight difference in the relative sizes. On the whole there is less size difference among the various spines of a single individual in the larval stages than in the adult, and the number is more constant. Careful examination of 25 cercariae from each of 3 snail hosts, fixed and cleared in glycerine, gave the following data: 72 with 37 spines, typically arranged; 2 with 1 of the dorsal aborals missing; and 1 with a dorsal aboral spine duplicated—giving a count of 38 for this individual. Accessory spines may have been overlooked, as they would be very small if present.

GENITAL SYSTEM.—The genital system is apparently very similar to that of all other species of the genus. The testes are usually regular in outline in unflattened fixed specimens but frequently are divided into 3-5 shallow lobes (Figs. 13, 14). In worms that have died in the host the inner parts of the testes pull away from the outer epithelium and give the appearance of a lobed testis, and worms that have been killed under pressure almost invariably have irregular testes. The vasa deferentia run into a large seminal vesicle which lies in the posterior part of the muscular cirrus sac. The anterior part of the sac is occupied by the pars prostatica, the voluminous prostate gland, and the well developed cirrus. The cirrus opens through a common pore with the metraterm, which runs along the right side of the cirrus sac in all specimens examined. Looss (1899, Figs. 5, 10) shows the uterus on the right side in one and on the left in the other figure. The position of the cirrus sac is usually anterior to the middle of the acetabulum and is often entirely anterior to it in the younger worms; in some cases it is entirely dorsal and reaches the posterior border of it (Fig. 14). The female system is also typical of the genus, having, instead of a seminal receptacle, a more or less voluminous receptaculum seminis uterinum. A fairly distinct Laurer's canal, a diffuse shell gland, vitellaria from acetabulum to the posterior end, and a small vitelline reservoir are also characteristic structures. The uterus is long, regardless of the age or maturity of the worm, and is coiled transversely into 7 or more loops. After it begins to fill with ova it usually does not have less than 9 loops, and more are added as the eggs increase in number. Barker (1916) has attempted to use the number of eggs in the uterus as a character on which to key the muskrat echinostomes. This is not a good character, however, for this species may have from none at all to over 6,000 eggs. The uterus in a 21-mm worm from a muskrat was teased out and the eggs counted. Each egg was counted as it was drawn into a pipette and in this manner 6,200 were counted and a hundred or more were probably left in the tissues. The number of eggs produced in 24 hours was also determined for several worms at different ages. In Transfer X (p. 64), a single immature worm

was taken from a rat and transferred to the cloaca of a pigeon. It matured and began producing eggs in 6 days, or when it was 18 days old. After it had been producing eggs for 7 days, a 24-hour fecal sample was taken, and by the dilution and direct count method the number of eggs was determined to be 4,100. The following day the count was 3,800 and the counts for the next 2 days were respectively 3,460 and 3,402. Similar records were taken on other transferred worms and the highest number for any one day was 4,600, which is more than 3 per minute. This count was made by the Rivas method (1932, p. 479), which was finally adopted as the most satisfactory for this type of work. Most of the worms produced 2,000-3,000 eggs daily to within a few days of death, and 700 per day is the least any worm produced. The 700 per day count was made on a worm 59 days old.

Egg size varies with the age of the worm and is possibly somewhat altered by the host. The younger worms produce eggs with a very great range in size, and the average length is much greater than in more mature ones. The range in size for the eggs of the worms from all hosts was found to be 91 to 145 μ by 66 to 83 μ . The largest were in the first positive stools of Cat 4 and the smallest were found in Muskrat 261, but those from some of the pigeons were almost as small as the ones from the muskrat. Usually the eggs from bird hosts are darker in color and appear to have a thicker shell but there are some exceptions to the rule, for those from muskrat hosts are usually almost as dark as the ones from the pigeon. Variability in the size and color is much too great to allow the use of this character in distinguishing *E. revolutum* from other closely related species.

The transfer experiments also gave some interesting data regarding the self-fertility of the species. On 10/24 Rat 26 was killed in order to get some immature worms for transfer. These worms were 12 days old, and so far as could be determined by means of microscopic examination of the living worms, all were sexually immature, having no sperm in either the seminal vesicle or receptaculum seminis uterinum. In fact the latter organ was not yet formed. One worm was transferred into each of 4 pigeons (T7, 8, 9, 10; see p. 64). Three of them gave positive stools on the fifth day after the transfer was made, and T9 lost its worm before it matured. About a week later 50-100 ova were collected from the feces of each pigeon and incubated in tap water. Normal miracidia developed in the eggs from each of the worms and the rate of development was the same as for those from hosts carrying an infection of several worms, so that cross-fertilization would be possible. The question as to whether trematodes are self- or cross-fertile is one that has received a good deal of attention. The only data to be found on it are occasional

reports of observations on worms with the cirrus inserted into either its own metraterm or into the genital pore of another individual (Looss, 1893). Where single individuals are found in the hosts it might be assumed that they were self-fertile if viable eggs were produced, but one could not be sure that a second individual had not been present earlier.

Morphological Variation Induced by the Host Species

In the preliminary experiments it was noticed that the worms from the various hosts had slightly different appearances, but these differences were in most cases so slight that they could not be described or figured. It became especially noticeable when worms from avian and mammalian hosts were compared, and since some confusion seems to be due to lack of understanding of this variability it was thought worthwhile to study it in more detail.

A fairly complete size series was obtained from both avian and mammalian hosts, and in order to compare all sizes of worms the most satisfactory method was found to be the graph system commonly used in biometric studies. Three graphs were used for the comparison of each character in most cases. One was used to show the number of individuals used and their measurements from the bird hosts and a similar one for those from the mammals. A third chart to show the partially smoothed curves was taken from the other two. This method indicates the range in all classes and the variability within the range; it gives the proportions of the worms at all sizes, and the differences in the worms from the two types of hosts. The significance of the differences can be judged directly from the plotted data. About fifty such graphs were prepared, but only twenty of the most illustrative have been included here.

Although there is a very marked difference in the size attained in the various hosts used in these experiments, *Echinostoma revolutum* apparently does not reach a definite size but continues to grow until it is expelled. The maximum size indicated in the charts does not express the absolute maximum size for the species but the actual size of the individuals studied. The curves were made by drawing straight lines through the points obtained by averaging the points within arbitrary limits of range. The worms from all hosts were fixed, stained, etc. in exactly the same manner in so far as it was possible. None were killed under pressure.

Various authors, notably Looss (1899), have suggested that much of the variation in this parasite may be due to the host species, but no one has to my knowledge attempted to measure or describe it.

One of the most conspicuous differences in worms from the two types of hosts is the greater reduction in the dorsal cuticular spination in the

worms from birds. While there is also a variation in those from each of the mammals and birds, the differences are less marked than when the bird- and mammal-reared worms are compared collectively (Chart 8). That the reduction in dorsal spines is not due to age alone is shown by the fact that it is not so easily correlated with spine reduction as is the body length. When the number of complete rows of dorsal cuticular spines plotted against the length of the worms is averaged and a curve drawn, a very pronounced contrast in the larger worms becomes apparent. For example, an 8-10 mm worm from a duck may be completely spineless on the dorsal side while on another of the same size from a rabbit or muskrat there may be 10-15 complete rows of spines. This is particularly important in the light of some of the definitions of the two genera *Echinostoma* and *Echinoparyphium*. Sprehn (1930, 1932) considers one of the differences in these genera to be the absence of dorsal cuticular spination in the former and the presence of it in the latter. Following this definition would necessitate putting the worms of this species into both genera.

The length of the cuticular spines was measured and plotted in Chart 7. Contrary to expectations, the spines are longer in comparison to body length in bird-hosts, and the difference is considerable. In the smaller worms the collar spines are longer in mammals, but in the larger worms the variability is so great that although they are probably also longer in mammals the data do not clearly indicate it.

Differences in body proportions are not very pronounced in most cases, but since there seems to be a significant variation in the same direction for all parts measured it is clear that some of the variation in shape in this species can be attributed to the different types of hosts. As a rule the worms develop more rapidly in birds (Table 7, p. 77), become mature earlier and at a smaller size, and live a much shorter period. The differences in proportion are shown in Charts 9-20. The worms from birds progress toward mature proportions more rapidly than those from mammals, making a rather pronounced difference in the younger individuals. There is less difference in those between 6 and 8 mm, but between 8 mm and the upper limits the differences become progressively greater, the worms from birds being generally wider and stouter than those from mammals. There is apparently not much difference in the size of the acetabulum (Charts 11, 12), but when the diameter of the oral sucker is plotted against that of the acetabulum a significant difference is observed (Chart 18). The larger worms from bird hosts have a relatively larger oral sucker. Similarly the collar is larger as compared with the acetabulum in the larger specimens from birds, and smaller in the shorter ones (Chart 17). Coincident with this variation is the difference in

growth rate in the two types of hosts mentioned above. It should be mentioned, however, that differences in body proportions are not great enough to make them readily discoverable by inspection. It is only when large numbers of individuals are compared biometrically that the differences become obvious. It is shown in Charts 9-14 that the variability within each group is sufficient to give much overlapping.

In one instance the variation due to the host was very conspicuous. The worms taken from the pig were barely mature after four weeks and the size of the various parts as well as the whole were very strikingly dissimilar to the average from the other hosts. The body is only 3.6-3.75 mm long and wider than normal. The acetabulum is large and the post-testicular region is much reduced. The testes and ovary are nearly equal in size and much too small, being slightly smaller than the pharynx. The spination on the collar is normal in number and distribution of spines but the length is greater than normal. The whole appearance of these worms is so different from the normal that they could easily have been described as a different species had their origin not been known.

It may be concluded that while there are very definite variations induced by the conditions within the various hosts, they are comparatively slight in most cases. However, they are conspicuous enough to account for some of the confusion in the literature regarding this species. It is particularly true of the cuticular spination and the total length attained, there being a range of from less than 4 to about 30 mm in the length of the worms producing eggs. The differences in proportion can be explained on the basis of differences in growth rate, but the differences in the character of the cuticular spination are as yet unexplained.

Hosts and Geographical Distribution

Echinostoma revolutum is one of the most cosmopolitan of trematode species, having been reported from every temperate region in the world with the exception of South Africa and inland China. It is also found near the equator but is apparently less common there. Tubangui (1932a, b) records it as fairly common in the Philippine Islands (Luzon), and Picard (1930) took an echinostome species from the pigeon in Java which is probably *E. revolutum*. The regions where it is known to occur are indicated in Tables 1, 2, and 3. Only the records that have been published since Kowalewski (1895) and Looss (1899) redescribed the species are used, and some of these reports are doubtful and have either been excluded or indicated as questionable.

This species seems to be as cosmopolitan in its choice of hosts as it is in geographical distribution. This lack of specificity in all of its parasitic stages is of course the most important reason for its wide

distribution. The experiments of Tsuchimochi (1924) and Anazawa (1929) in which they infected certain mammals suggested that this species might also occur in mammals in nature. My own experiments have confirmed those of Tsuchimochi and Anazawa and added many new experimental hosts; a number of new records of natural infections in mammals and birds have also been obtained. Tables 1, 2, and 3 give the hosts, distribution, and references for the incidence of the cercaria, metacercaria, and adult, respectively.

Cercaria Echinostomi-revoluti is known to occur in at least four genera and ten species of pulmonate snails. Although it may be found in several species of a particular region it seems to be decidedly more prevalent in a single species. In the vicinity of Urbana, I have searched for it in *Physa gyrina* for three years and have never found a single infection. Miller (1936), who made more extensive collections in the same region, has given but a single record of it from a stream where the incidence is particularly high in *Helisoma trivolvis*. The percentage of infection in *P. gyrina* in this region is probably much below 1 per cent while in the same region it is as high as 60 per cent in *Helisoma trivolvis* during the summer months.

The agamodistome may occur in any of a very great variety of hosts. In this study a number of attempts were made to determine the most "natural" hosts, and for this particular region it seems that they are *Physa gyrina*, *Helisoma trivolvis*, and *Rana pipiens*, named in the order of frequency of natural infection. *Helisoma trivolvis*, which also serves as the primary intermediate host, carries a rather high percentage of infection in nature, but not as high as it was at first thought; an erroneous idea regarding this is easily acquired if care is not taken to insure against laboratory infections of the snails examined. By carefully drying each snail as it was collected in the field and isolating it in the laboratory or by examining it immediately, I found that in the one region which received most of my attention *Physa* is probably the most natural host. Six adult *Rana pipiens*, 6 half-grown tadpoles of the same species, 4 medium-sized *Physa gyrina*, and 6 small *Helisoma trivolvis* were collected from the same bend of a stream, all on the same day, and examined for cysts of *E. revolutum*. Each cyst from the frogs and most of those from the snails were pressed under a coverslip and carefully examined. The results are shown in tabular form:

Host	Number of Cysts	Number of hosts positive
Adult <i>R. pipiens</i>	2 to 27	4 out of 6
Larval <i>R. pipiens</i>	6 to 41	4 out of 6
<i>Physa gyrina</i>	12 to 125	3 out of 3
<i>Helisoma trivolvis</i>	1 to 18	6 out of 6

When tadpoles and the two species of snails, all laboratory raised, were put into a small aquarium with active cercariae, the tadpoles seemed to get the largest share of the parasites and the *Helisoma* the least. It was found that it was necessary to govern carefully the infections in the tadpoles and *Physa* for they would become so heavily infected in a few hours that they would soon die. On the other hand the *Helisoma* very rarely died because of heavy infection with metacercariae. Heavily infected tadpoles became swollen and died with a sort of general edema. Lutz (1924) made the same observation on tadpoles infected with *Echinostoma nephrocystis* (?—*E. revolutum*). The following experiments will serve to illustrate how readily the cercariae enter and encyst in tadpoles. A laboratory raised tadpole (*R. pipiens*) about 25 mm in length was put into a 200 cc container with 75 freshly emerged cercariae and left for about one hour. They were observed from time to time, and on one occasion 7 cercariae were seen creeping around within the transparent cloaca. The following day the tadpole was dissected under the binocular microscope and 53 cysts found in the kidneys and adjacent ducts, and 7 cysts were found in the gill chamber. Many other tadpoles were infected and used in the feeding experiments. A half-grown hairless rat (Rat 27), for example, was fed a 30 mm tadpole that had been in a finger bowl with an infected snail (C6-9) for about 2 days, and 431 worms were recovered from it. Two small *Physa* were also infected from snail C6-9, and fed to Pigeon 15 from which 63 worms were recovered (Tables 5 and 6). There can be no doubt that Tsuchimochi (1926) and Fallis (1934) are correct in their statements that *Echinostoma revolutum* will use either a snail or a tadpole, depending upon which is available. There is apparently very little difference in the two species of tadpoles used in the experiments; the larvae of *Rana catesbiana* were as easily infected as *Rana pipiens*. *Pseudosuccinea columella* and *Fossaria modicella* were also easily infected. It was also possible to get infections in several more unusual hosts. Five *Sphaerium* sp. and 3 *Pisidium* sp. were exposed to heavy infusions of cercariae for 8 hours and examined after 24 hours and 5 days, respectively. In one *Sphaerium* 14 cysts were found, but in the same individual 22 of the cercariae had lost their tails and were still creeping around under the mantle; another had 9 cysts and 18-20 unencysted cercariae; one had 6 creeping and none encysted, and the other two, which were smaller individuals, had none. Eight cysts were counted in a *Pisidium* five days after it had been exposed for eight hours. Two others of the same lot were negative and one had only two cysts. The cysts when present were in the flesh of the clam near the hinge in both species. Several species of scaly fish were exposed and examined but none were ever found positive. It is probable, however, that the catfishes are sometimes natural hosts, for the two

experiments with the black bullhead, *Ameiurus melas*, indicate that the cercariae react to it very much as they do to the tadpoles. A fish that was about 8 cm long was put in a shallow dish with 250-300 cercariae and left for eight hours. When it was dissected the next day 67 cysts were found deep in the substance of the kidneys, 4 in the left mesonephric duct near the kidney, and 9 in the same duct near the cloaca—a total of 80 cysts. They were all normal in appearance having well formed walls, and the host did not appear to be suffering ill effects. A second fish of the same species was left in a shallow dish in 1 liter of water with an infected snail for 4 days. On the last day it was somewhat bloated and very inactive and finally died. Several hundreds of cysts were found in the kidneys and associated ducts.

In the experimental work done thus far on *Echinostoma revolutum*, including the present study, it has been shown that 14 or 15 species of snails may serve as secondary intermediate hosts, and none of the other species of snails have been experimentally excluded as possible hosts. Johnson (1920) has made the only unsuccessful attempt to infect tadpoles. At least four species—*R. pipiens*, *R. catesbiana*, and the "tadpoles" of Tsuchimochi (1926) and Fallis (1934, *Bufo americana*)—are known to carry infections of this species. Miki (1923) found cysts in *R. esculenta*, which he fed to rats and mice and recovered *E. cinetorchis* (= *E. revolutum*). According to Ando and Ozaki (see Dollfus, 1925, p. 90) the metacercariae of *E. cinetorchis* (= *E. revolutum*) were found in *Rana nigromaculata*, *R. rugosa*, and *R. japonica*, which increases the number to seven or eight known amphibian hosts if *E. cinetorchis* is accepted as a synonym of *E. revolutum* (see p. 47). *Ameiurus melas*, which is shown by this study to be a probable natural host, is the first fish to be reported as a host for this species.

The adult worm apparently may be found in almost any bird or mammal (Table 3). Natural infections are, of course, limited to those animals that feed upon aquatic animals, but many others may be experimentally infected and act as "normal" hosts if not "natural" ones. In the present study an effort was made to discover the host which would serve as the most satisfactory one for routine culturing of this species, and incidentally the pig was infected to determine the effects produced by the larger host. These experiments are outlined in another section (p. 56) and summarized in Table 6. For culturing the worms rapidly the pigeon or guinea pig are the best adapted, but greater size is attained in the duck or rabbit. The rats and mice used were found to be undependable; and although the worms develop as well in the dog and cat, these hosts require more space and attention and were for that reason less often used. Although the worms develop slowly and attain a smaller size in the domestic pig, in view of its habits it may be expected to harbor natural infections of *E. revolutum*.

Immunity Phenomena

Although only a few experiments were designed specifically to test the types or degree of immunity developed in the various hosts used, the large number of infections and variety of hosts used has lead to certain new conclusions and confirmations which are being reported even though they must in most cases be repeated and extended before the results are accepted.

Table 5 and 6 (pp. 72-76) indicate the number of hosts used in the first series of experiments. The number of hosts from which no worms were recovered or were at least not known to be infected are also given here. In most of the hosts reported negative, it is certain that the worms remained in the gut for a few days and in some cases were lost only shortly before maturity was reached. Those hosts reported negative are, then, those which contained no worms when autopsied or did not produce stools which were found positive by fecal examination.

It may be seen from Table 6 that all attempts to infect cats, dogs, chickens, hogs, and guinea pigs were successful. Very few of the pigeons, ducks, or rabbits were negative, but the mice and rats could not be relied upon to hold the worms. This is particularly true of the albino and hooded rats, in which no infection was accomplished in 14 attempts. On the other hand, large mature worms were taken repeatedly from wild and hairless rats.

All of the rats were treated similarly. The diet after the experiments began was the same for all and they were fed in all cases as much food as they would eat. They were obtained from the "discards" at the Animal Breeding Laboratories at the University of Illinois. Unfortunately, the history of these rats was not obtained, as it was not thought to be sufficiently important at that time. Accurate data on the diet and the pedigree of each rat would, however, have made the experiments of greater value since these factors probably account for some of the "natural immunity" displayed. Ackert *et al* (1931a, b) and others have shown that vitamin deficiencies alter the natural course of infections, and since other researchers (Tsuchimochi, 1924) have reported infecting laboratory rats with *E. revolutum*, it seems even more likely that under different conditions the rats used in these experiments would have been more consistently positive. Tubangui (1932b) had similar experiences. He was using pigeons and albino (?) rats in his experiments and fed cysts of *E. revolutum* to both. While the pigeons were always positive the rats were in each case negative. His rats may also have been maintained on a diet which rendered them nonsusceptible.

The results obtained from the mice are not particularly significant in this connection as it was not possible to determine whether the wild

ones actually ate infected snails or not; and all of the positive mice either died in a few days after infection or were killed before the worms matured.

In regard to natural immunity it may be concluded that among birds it is practically nonexistent, and although the albino rats seem to demonstrate some natural immunity none of the other mammals have been experimentally excluded from the list of possible hosts for this species of echinostome.

A few experiments were carried out to determine whether or not an acquired immunity to reinfection could be demonstrated in pigeons. It was demonstrated that pigeons usually lost their infections in about three weeks. In one case (Pigeon 14) in which the infection was lost after 15 days (many eggs had been present in the feces for five days) and the pigeon reinfected two weeks later, only one very immature worm was recovered on the eighth day. An abundance of cysts (100-150) had been fed both times, and the diet was not changed. These results indicated that this pigeon had either acquired an immunity to reinfection or that the diet used over the long period of time was unsuitable for the parasite.

The following is a summary of the experiments which followed this observation.

Pigeon Im 1 had been used as T2 and T4 (p. 63). As T2 it had received *per anus* 5 worms that had lived 18 days in Rabbit 7, and it carried this infection for six days. As T4 it had likewise received 10 worms 14 days old from Pigeon 18. It carried this infection for 12 days. Transfer 2 was made on 10/3/33, and the other transfer was made just two days after all of the worms had been lost. On 11/2, or eight days after the last of the T4 worms had been lost, it was fed a Physa carrying an abundance of one-day-old C7-1 cysts (see p. 63). No ova were found in the feces, although careful daily examinations were made from 11/13 to 11/22. On 11/22 it was fed 35 of the C7-1 cysts that were twenty days old. These were teased out from the Physa and administered in a small capsule. Daily fecal examinations from 12/1 to 12/15 were made and no eggs were found. The host was killed on 12/15 to determine whether the worms were present but retarded in development. No worms were present.

Pigeon Im 2 had been used as 14 and T6. As 14 it had been fed C6-12 cysts on 10/15. Ova appeared in abundance on 10/15 but disappeared on the fifteenth day (10/20). As T6 it had received *per anus* on 10/24 a single mature worm that had been in Rat 24 for 39 days. This worm lived only six days in Pigeon Im 2, and produced ova in fair abundance until it was expelled on 10/30. On 11/2 it was fed two snails, each carrying about a hundred cysts that were 1-3 days old. No ova were discovered by daily fecal examinations from 11/12 to 11/23. On 12/6 it was again fed about 125 cysts that had been in the snail host for 48 hours. Eight days later it was killed and a single very immature worm only 2.5 mm in length was recovered. This is about one-half of the length normally attained in this time.

Pigeon Im 3 had been used as T3. As T3 it had received *per anus* on 10/8, ten worms that had matured in Dog 3 (23 days). It carried these for 24 days, or until 11/1. On 11/2 it was fed a snail with about a hundred cysts one day old.

Ova were first found on 11/12 or on the tenth day and continued to the sixteenth day. No ova were found on 11/19 or thereafter. It was fed two snails each carrying about 75 cysts two days old on 12/6. On 12/16 it was killed and three very immature worms (1.6 to 1.7 mm in length) were recovered.

Pigeon Im 4 had been used as T1. As T1 it had received *per anus* on 10/2, six mature worms from Chicken 5. It carried these worms until 10/28, or 26 days. On 11/2 it was given a snail with about a hundred cysts one day old. A few ova were found in the feces on 11/18. This was the sixteenth day after feeding, which is four to six days later than normal. The ova were present in very small numbers until 12/5, or the 33rd day. On 12/6 it was again fed about one hundred cysts in a *Physa* and killed nine days later. It was negative.

Pigeon Im 5 was used as T10. It had received *per anus* one immature worm from Rat 26 on 10/24. The worm was expelled on 11/22, or 28 days later. This worm had been in the rat host for twelve days. On 12/10 it was fed a snail with 78 cysts that had been encysted for two, three, and four days. It was positive by fecal examination on the seventeenth day and was killed the next day (12/28). Two small mature worms were recovered.

Pigeon Im 6 was used as T5. It received one mature worm from Pigeon 19 *per anus* on 10/18 and carried it until 11/28, or for forty days. This worm had been in Pigeon 19 for 21 days. On 12/10 it was fed a small *Physa* with about forty cysts two days old. It was positive by fecal examination on the twelfth day and subsequently until it was killed on 12/31, the 21st day. Eleven mature worms 8 to 8.8 mm in length were recovered.

Pigeon Im 7 was used as T7. It had been given *per anus* one immature worm from Rat 26 on 10/24. The worm was expelled on 11/14, or twenty days after the transfer was made. On 12/10 it was fed a snail with 22 cysts one day old. Ova were never discovered in the feces, and it was negative when killed on 12/27.

Pigeon Im 8 had been used as T9. It received *per anus* one immature worm from Rat 26 on 10/24. The worm was expelled before it matured, probably immediately. On 12/10 it was given a snail with 150-200 cysts. Ova were not found in the stools until the nineteenth day. It was killed the same day (12/29), and a single mature worm 6.95 mm long was recovered.

At the termination of the experiments the hosts had been in captivity, held in small cages 2' x 2' x 3' for the following lengths of time: Im 1, 8 weeks; Im 3 and 4, 10 weeks; and Im 2, 5, 6, 7, and 8, about 12 weeks each. These experiments are summarized in Table 4.

There is a good deal of variation in the behavior of the eight re-infected pigeons. It seems to be generally true that the rate of development is decidedly slower in the second and third infections. The average time for the appearance of positive stools in first infections is ten to twelve days, but the time required in the second infection for Im 4 was 16 days; for Im 5 it was 17 days, and in Im 8 ova appeared in the stools on the nineteenth day. However, in the case of Im 3 eggs were found on the tenth day and in Im 6 on the twelfth, which would seem to contradict the conclusion that the pigeons acquire a sort of immunity that retards development. There is still a further contradiction offered by Im 8 in which the one worm administered *per anus* in the first infection

did not remain long enough to be really considered as an infection, and yet there is no essential difference between the second infection in it and that of Im 5, whose first infection lasted for 28 days. In both cases the rate of development was about equally retarded.

The number of worms present in the first infection is ruled out as a factor influencing the second one by the fact that Im 1, which had only a total of 17 worms for a period of 18 days, was refractory to both subsequent infections; while Im 3 had carried ten worms for 24 days and several more for a second period of 16 days, and although the rate of development was somewhat retarded in the third instance, an infection was accomplished.

There is some possibility that the age and number of the cysts fed are factors influencing the character of the infections, but they are probably minor ones, since in the first infections in these experiments and in the infections used in other experiments no noticeable difference appeared in cases where cysts ranging from one day to three weeks old were used. The slight metamorphosis that occurs after the cercaria encysts is accomplished very rapidly, and the metacercariae are infective almost immediately after encystment. In Experiment 11, for example (p. 61), Rat 27 was given cysts less than 36 hours old, and 431 worms were recovered from it.

Because of such marked uniformity in the first infections in all of the pigeons used, age immunity is considered to be of very little importance. The pigeons were taken without regard for age.

While the data may be interpreted as indicating some immunity reactions it seems more probable that the diet of the hosts and the conditions under which they were maintained in the laboratory more satisfactorily explain the phenomena observed. In the case of the first and single infections the pigeons were taken from a barn where they could choose from a variety of foods, exercise freely, and follow a normal daily program. When they were brought into the laboratory they were held only long enough to determine by fecal examination whether intestinal parasites were present and to get them to feed. The diet used was fairly uniform throughout the whole series of experiments, i.e., all the hosts were given the same foods in nearly equal proportions. The diet consisted of yellow corn, wheat, oats, and a little rice. Although pronounced haemorrhagic enteritis was produced in a few cases (in the experiments to determine the general nature of infection in the various hosts), none of the pigeons used in the immunity experiments ever lost weight noticeably but appeared to maintain excellent health throughout the length of the experiments, which lasted for three months in some cases. However, there was a decided change in the character of the

feces after a month or two in captivity, which indicates that there was a change in the general condition of the host. During the first few weeks the normal stool contained considerable greenish material regardless of the type of grain fed. A few weeks later it became a pale green and finally a greyish yellow with an occasional greenish tinge. This of course varied greatly with the various individuals and in the case of Im 6 the stools continued to be greenish during the whole period. It was also noticed that some of the pigeons were considerably more restless than others, thus introducing another variable, the amount of exercise. Im 6, which was the most restless of all, was the most normal with respect to the type of stools, and was the only one to carry what could be considered a normal infection after a long period of captivity.

I do not propose to attempt an explanation of these phenomena, but in passing it is interesting to note again that the diet consisted largely of yellow corn with some wheat, oats, and a little rice. The pigeons were never in direct sunlight after they were captured and were not allowed to exercise more than was possible in the small cages. The diet was not made up with any regard for vitamins and must certainly have been deficient in vitamins A and D, and as soon as the hosts' reserves were exhausted they would be deficient from that time on to the end of the experiments. Ackert *et al* (1931a) found that chickens maintained on a vitamin A free diet developed more and larger *Ascaridia lineata* than controls that were fed on balanced diets. This was interpreted as a result of lowered resistance induced by the vitamin deficiency. The diet used in those experiments differs considerably from that used in mine, and the hosts in Ackert's experiments were irradiated. In another series of experiments (Ackert *et al*, 1931b) similar results were obtained with vitamin B free diets. In the conclusions to the latter report it was suggested that there may be a direct effect of the diet upon the parasite rather than upon the resistance of the host. That the experiments of Ackert differ greatly from mine both with respect to experimental material and methods is, of course, recognized. However, since in both cases vitamin deficient diets were involved and since they led to diametrically opposed conclusions, it is worth while to point out again that instead of the resistance of the pigeons being lowered or the parasites being benefited by the diet and lack of sunlight or exercise, the opposite was generally true in my experiments. The parasites either did not develop at all or were decidedly retarded in their development.

The transfer experiments provide some interesting facts relative to the topic of immunities in that there seems to be a definite increase in the longevity of the worms by transferring them from one host to another. These experiments have been described and summarized in

Table 9 (p. 77). The average duration for heavy and light infections alike is about three weeks for the first infections in pigeons. In six of the ten transfers the worms lived 20 days or longer in the second host, and in Transfer 3 the one worm that was taken after it had lived its expected limit in the first host, lived an additional forty days in the second. In Transfer 4, in which the infection lasted only twelve days, the pigeon which served as the second host had already been used in Transfer 2, in which it had carried five worms for six days. This would seem to show that the pigeon used in Transfers 2 and 4 had more than the average resistance and should be compared with the others on that basis.

Since no other transfers such as those described here have been made, it is not possible to broaden the conclusions by comparisons. Unfortunately, they were few in number and for that reason merely indicate rather than decide the above question as to whether or not there is a sort of accumulative immunity developed which limits the length of the parasite's life.

In all the experiments which have a bearing upon the question of immunity a good many factors have not yet come under consideration. Taliaferro (1929, p. 247), in his extensive treatise on "Immunology of Parasitic Infections," points out that age as a factor independent of all others is often an important one and more especially in cases where the host is an unnatural one. Since there are so many hosts for *E. revolutum* and quite an extensive list of both birds and mammals from which it is repeatedly taken in nature, it is hardly possible to decide whether the pigeon should be considered a natural or incidental host. There have been numerous reports of natural infections of echinostomes in pigeons (Müller, 1897; Krause, 1925a; Bolle, 1925; Zunker, 1925; Heelsbergen, 1927; Sprehn, 1927, 1930; and Picard, 1930), and while most of them were either determined only to genus, identified as new species, or species closely related to *E. revolutum*, it is more than probable that in many cases the worms dealt with are identical with *E. revolutum*. This has been discussed at length in another section (p. 51). Notwithstanding these facts it must still be maintained that the pigeon is relatively incidental as a host for this species or any other trematode parasite whose occurrence in the pigeon's gut is dependent upon its having fed upon aquatic animals or vegetation. Furthermore, pigeons as a rule spend so little time around bodies of water that it is most certainly true that the snails from which the cercariae emerged to infect the second intermediate host, which the pigeons ate in order to become infected, probably were not in the first place infected by miracidia which hatched from eggs that were dropped by pigeons. If the pigeons may be considered to be

more or less incidental hosts, then they might also be expected to show some age immunity. In a few cases it was possible to determine that the pigeons used were scarcely more than "fledglings," but in most cases it could only be noted that they were relatively old or young. Some of the lack of uniformity may then be due to this difference in age although it is probably a relatively minor factor, since there was a very striking uniformity in the pigeons that were used soon after they were captured.

Taking all of these factors into account there seems to be some evidence that although the prolonged captivity and unsuitability of the diet produce more obvious reactions which tend to obscure the immunity phenomena, the pigeon does develop a slight immunity to *Echinostoma revolutum*, as indicated by the transfer and reinfection experiments.

Discussion of Related Species and Synonyms

In the newer literature there are at least eighteen species which according to the descriptions have about 37 cephalic spines. After having made a detailed study of the diagnostic characters in a complete series of worms from a variety of hosts, I had expected to be able to clear up some of the confusion regarding these species. I am doubtful, however, whether this single attempt will lessen the number of questions regarding synonymy, for while it does reduce several of the described species to synonymy it also shows that many others that might have been carried along in the literature as valid species must now be considered doubtful until they have been reinvestigated. This in itself would not be particularly noteworthy if in all cases the type specimens were available, but this is not so in many instances.

It was my original intention to restudy the descriptions of all closely related species and possible synonyms, but after having worked at length on the older literature I was convinced that it is indeed impossible to determine from the figures and descriptions of most of the earlier authors whether they had studied this or some other species. Furthermore, if I were able to reach a conclusion regarding them I would merely add another "opinion" to the already extensive list. There is even much doubt in my mind that the laws of priority have been correctly followed in the naming of *Echinostoma revolutum*. After examining Froelich's description (Froelich, 1802) and figures of his "*Fasciola revoluta*" (see Fig. 26), I am very much less convinced than Dietz (1910, pp. 293-296) that Froelich actually studied this species. At least I cannot agree with him that he was justified in changing the name "*echinatum*," which had already been in use for over a century. Dietz's argument merely indicates that Froelich's worm could possibly have been the same as *E. echinatum* and does not prove that it was beyond reasonable doubt

identical. "*Echinostoma revolutum*" has been accepted now and used as the correct name for this species since 1910, and irrespective of opinion regarding priority and propriety I would not propose further change in the nomenclature for *Echinostoma revolutum*. *Echinostoma echinatum* (Zeder, 1803) is then listed as the first synonym of *Echinostoma revolutum*. Other synonyms which have been generally accepted, although they have not and cannot be demonstrated as such, are *Distomum oxycepalum* Rud. 1819, *Distomum dilatatum* Miram 1840, and *Distomum armatum* Molin 1850 (see Hassall, 1896). I have examined the original descriptions of each of these and agree that they could all be identical with *E. revolutum*.

Only two of the eighteen forms which have been described as having about 37 cephalic spines can be definitely distinguished from *Echinostoma revolutum*. Eight of them are questionable species and the other eight are probably synonyms. The two species which are easily distinguished are *Echinoparyphium aconiatum* Dietz 1909 and *Echinoparyphium contiguum* Barker and Bastron 1915. The very short uterus in these forms readily separates them from all members of the genus *Echinostoma*, and the relative size and arrangement of the cephalic spines further distinguishes them. It is doubtful whether they can be separated from each other, however. Studies were made on numerous specimens of *Echinoparyphium* sp. from the muskrat which is the host for *Echinop. contiguum*, including two specimens identified as *Echinop. contiguum* (accessioned in the collection of the B. A. I. of the U. S. D. A. as #30851). All of them have many more than 37 spines, having 45 in some and 47 in others.

I believe that it is unquestionably true that the number and above all the arrangement of the collar spines serve as the most reliable characters for diagnosis of closely allied species. Kowalewski (1895), Dietz (1910), Tubangui (1932a, b), Rasín (1933), and many others seem to hold the same opinion. On the other hand some have argued, notably Looss (1899), that there is too much variability in the spines to permit diagnosis on this basis. Looss, however, did not consider the arrangement of the spines in more detail than the alternating rows and grouping of the spines of the ventral lappets. Other characters which have been used are the extent of the vitellaria and the location of the worm in the host. The character of the vitellaria is too variable with age to be of value, and the position within the host although fairly constant for a species is altered very considerably by the number of worms present and the length of time elapsed between the host's death and the autopsy. The presence or absence of cuticular spines also depends upon the latter condition since dead worms frequently slough off the whole cuticula. The

stoutness of the body and general shape depends too largely upon the host, age, diet of the host (?), time of autopsy, and type of fixation to be of very great value in diagnosis. The most constant characters have already been described in another section (p. 18). As a result of the present study the following characters have been adopted as of diagnostic value: number of collar spines; relative size of the various spines; their arrangement in the $(2 + 3) + 6 + (8 + 7) + 6 + (3 + 2)$ fashion; the length of the uterus; and the relative size of the two suckers and the pharynx. In my opinion the host species is not to be regarded as important in this parasite.

In studying the descriptions of closely allied forms, the above characteristics have been used as a basis for conclusions regarding relationship. Other characteristics such as size of the body, eggs, and gonads have also been noted. The eight doubtful species mentioned above are those that have been described as having 37 spines, but the data given is insufficient to separate them from or identify them with *Echinostoma revolutum*; or, as in the case of *E. sudanense*, the description and the figures do not agree and one or the other seems identical with this species. In addition to *E. sudanense* Odhner, 1911, the doubtful species are: *E. acuticauda* Nicoll, 1914; *E. callawayensis* Barker and Noll, 1915; *E. erraticum* Lutz, 1924; *E. neglectum* Lutz, 1924; *E. microrchis* Lutz, 1924; and *E. echinocephalum* (Rud., 1819). These species of dubious standing and those that are shown by this study to be identical with *E. revolutum* will be discussed in detail.

Echinostomum sudanense, Odhner, 1911 (? = *E. revolutum*).—*Echinostomum sudanense*, described by Odhner (1911, pp. 116-117, pl. 3, figs. 12, 13), is based upon a single mature specimen from the rectum of a "Sattelstorch," *Ephippiorhynchus senegalensis*, and an immature specimen from the intestine of *Scopus umbretta* in North Africa. It is 6.5 mm long, cuticula spiny on the ventral side only, uterus long and the eggs numerous; length of pharynx equal to the diameter of the oral sucker; oral sucker about one-third the diameter of the acetabulum. All of these characters agree with specimens in my own collection taken from ducks. The collar spines are described as "31 schlanke und spitz Kragentacheln sind vorhanden, von denen 4 in jeder der ventralen Ecken sitzen und die übrigen 23 in einer doppelten, ununterbrochenen Reihe angeordnet sind." His figure 13, which I have copied (Fig. 27), shows 33 instead of 31 spines and the arrangement is strikingly similar to that of *E. revolutum*. The corner spines, which Odhner described as being four, are distinctly five on the left side of the figure, and on the right side the most lateral of the three oral corner spines is shown over on the adjacent one. This specimen was flattened under a cover glass and the spines somewhat

displaced, but it still resembles *E. revolutum* so closely that I am of the opinion that some of the spines were lost and that *E. sudanense* is really *E. revolutum*. There are at least two points on the figure where spines seem to be absent (cf. Fig. 27, 9; and Text-figs. 1-5). It is possible that it is a distinct species, but since the description is based on a single mature flattened specimen and the corner spines are so nearly identical with *E. revolutum* as are also the others in the unalternating laterals and alternating dorsals, it should be considered a probable synonym until more information on it is obtained.

Echinostoma acuticauda Nicoll, 1914 (? = *E. revolutum*).—This species was described by Nicoll (1914, pp. 110-111, pl. 6, fig. 4) from the straw-necked ibis, *Carphibis spinicollis*. It is a 37-spined form which from the description alone cannot be differentiated from *E. revolutum*. Nicoll states that *E. revolutum* is "altogether a much broader and bulkier form." It has already been pointed out that *E. revolutum* is bulkier and stouter in ducks than in other hosts and that it is quite delicate and slender in some. As these specimens were taken from the ibis they might be expected to differ from the ones seen in the duck. The figure of Nicoll's species resembles very much specimens which I have taken from the guinea pig or specimens taken from any host after they have been dead for some time. It is probably not as similar to *E. revolutum* as the description indicates, but since the cephalic spines are not described it is not clearly a distinct species.

Echinostoma callawayensis Barker and Noll, 1915 (? = *E. revolutum*).—This species was described from a collection of parasites from the muskrat, *Ondatra zibethica*, from Nebraska. It is described as having 37-41 cephalic spines; 31-33 on the rim and 2-5 on each flap. This variability in number suggests at least one of the two following conditions: either the material was in such poor condition that the spines were lost on some of them, or more than a single species was used for the description. I have not been able to examine Barker's material, but the figures and description lead me to the conclusion that small *E. revolutum* and *Echinoparyphium* sp. were both used in describing *E. callawayensis*. There has been only one record of this species since it was described (Law and Kennedy, 1932). Unfortunately the cephalic spines are not included in the description, and no specimens could be procured. In the figure given by Barker the posterior end is very much flattened so that the testes appear to be very large and the post-testicular region much shorter than normal for *E. revolutum*. The whole of the body looks more like *Echinoparyphium* than *Echinostoma*. The figure given by Law and Kennedy (1932, fig. 10) is, on the other hand, distinctly an *Echinostoma* sp. If *E. callawayensis* is a valid species it must at present be separated

from *E. revolutum* on very unreliable characters, particularly since the description is made from compressed specimens. I am not able to distinguish this species from related forms. In his key to the parasites of the muskrat, Barker (1916, p. 183) separates it from the other species on the compactness of the uterus. Since this character depends upon the degree of maturity and extent of contraction it is not safe to use it for diagnosis. Law and Kennedy (1932, p. 19) do not make any statement regarding the distinguishing characters.

Echinostoma erraticum Lutz, 1924 (? = *E. revolutum*).—Lutz, (1924) described a number of new echinostomes from South America, several of which are described as having 37 cephalic spines, and the collar of spines is left entirely undescribed in one of them. Four of these species are probably synonyms of *E. revolutum*. *Echinostoma erraticum* is so named because of its showing so little choice in its hosts, which is very definitely a characteristic of *E. revolutum*. Lutz found that *Physa rivalis*, *Planorbis* sp., and *Spirulina* sp. serve as hosts for the metacercaria, and if these are fed to pigeons, *Gallinula galeata*, *Chamaepelia passerina*, or *Aramides cayennensis*, adult worms may be recovered from each of them. He also found natural infections in *Creciscus viridis*, *Nycticorax violaceus*, and *Crotophaga ani*. He found specimens up to 8 mm in length, and his figure shows no characters not found in *E. revolutum*. The only statement regarding the cephalic spines is that the number varies from 35 to 39, with 37 as the usual number. In this same paper Lutz reports researches upon *E. revolutum* but does not make any statement regarding the specific characters by which he recognizes each of the several 37-spined species. I cannot find any characters to distinguish it from other species. The redia is also similar to *E. revolutum*, having a short gut and posterior appendages. According to the description, the 37-spined cercaria is in every respect identical with *Cercaria Echinostomi revoluti*.

Echinostoma neglectum Lutz, 1924 (? = *E. revolutum*).—This species looks very much like *E. revolutum* in the figures, but the description does not include any of the important diagnostic features. It is stated (Lutz, 1924, p. 87) that it can be distinguished from *E. erraticum* by the shape of the testes. As the shapes figured for both species are common in *E. revolutum* it is doubtful if *E. neglectum* is a distinct species.

Echinostoma nephrocystis Lutz, 1924 (? = *E. revolutum*).—*Echinostoma nephrocystis* is a form with which Lutz was able to infect tadpoles. He fed these to *Aramides cayennensis* and recovered the "new species" with 37 spines. The description is too incomplete to allow a decision as to the specific characters for it. Lutz seems to consider the host a distinguishing character. He says that it is most similar to Dietz's *Echin-*

ostoma distinctum which is a form with 35 rather than 37 spines. There is no question about its being a doubtful species and there is a very great probability that it is identical with *E. revolutum*.

Echinostoma microrchis Lutz, 1924 (? = *E. revolutum*).—This is another of Lutz's 37-spined species. The description of it is based upon several young specimens from *Gallinula galeata* and one mature one from *Creciscus viridis*. It is characterized as follows:

Der ausgewachsene Wurm enthaelt zahlreiche Eier. Seine Laenge betraegt nur 5 mm bei einer Breite von 1 mm. Der Stachelkranz enthaelt 37 Stacheln in der gewoehnlichen Anordnung; vom freien Ende aus gezeehlt, ist der fuenfte der laengate. Stachelschuppen sind zahlreich und auffallend bis auf die Hoehe des Ovariums, nachher werden sie seltener und undeutlicher.

This description fits exactly the average 5 mm *E. revolutum* from birds, particularly those that are contracted or slightly flattened. The statement regarding the longest spine is especially characteristic of *E. revolutum*; in fact in every one of several hundreds of specimens examined the most lateral one of the aboral corner spines is the longest (Text-figs. 1, 3, 5). He says further:

. . . die neue Art unterscheidet sich leicht von allen beschriebenen, da sie selbst in erwachsenem Zustande sehr kleine Hoden besitzt. Dagegen ist das Ovarium bedeutend grosser und voluminoeser, als bei verschiedenen ashnlichen Arten. Es ist kugelig und liegt mit seinem Hintertande dem mittleren Querdurchmesser auf. Die Hoden liegen ziemlich weit zurueck, aber nahe hintereinander. Die Vitellarien sind lang und anastomosiren briet zwischen dem zweiten Hoden und den Enden der Blinddaerme.

Lutz's figure of this species shows the one mature worm which he collected, and it is clear that the specimen is somewhat flattened and comparisons of relative sizes of the parts are therefore uncertain. In spite of this, however, it is clear that the specimen is indeed different from the average *E. revolutum*. I have never seen a specimen whose ovary is one and one-half times larger than the testes, but a number of the barely mature specimens have all three of the gonads about equal in size. The testes of Lutz's worm are considerably larger than the pharynx, and the uterus contains about 150 eggs. I have specimens of *E. revolutum* which also have small testes and consider them as slightly more abnormal than Lutz's worm. The testes in one of these specimens are slightly smaller than the pharynx and the uterus contains fifteen eggs. The ovary in this specimen is only slightly smaller than the testes. Since Lutz found but one mature specimen of this type and such abnormalities in the gonads are known to occur, I believe that the similarities in his specimen and *E. revolutum* are striking enough to almost, if not actually, establish their identity. If it is shown that a form exists in which the testes are consistently smaller than the ovary, then it may be distinguished from *E. revolutum* on the basis of that character.

Echinostoma echinocephalum (Rud., 1819) (?—*E. revolutum*).—*Echinostoma echinocephalum* is also a 37-spined species. It was originally described by Rudolphi (1819) and redescribed from the type material by Dietz (1910, p. 303, Pl. X, fig. 4, text fig. C). The specimens are immature, only 2.7 to 3.3 mm in length. The width of the head crown is 0.23-0.27 mm and body width at the level of the acetabulum is 0.47-0.60 mm. The head crown contains 37 spines described by Dietz as follows:

Davon liegen wie bei *Echinost. revolutum* 27 Stacheln in einer doppelten Reihe am Rande des Kragens; dieselben sind gleichgross, 0.0544-0.0720 mm lang und 0.012-0.0144 mm breit. An den beiden Enden dieser Stachelreihen befinden sich beiderseits in den ventralen Eckklappen noch je eine Gruppe von 5 Stacheln, von denen je 2 paarweise übereinander gelagert und ein fünfter einzelner Stachel median neben dem innern Stachel der vordern Reihe dieser Gruppe gelegen ist. Diese Eckstacheln sind im Gegensatz zu *Echinost. revolutum* (bei denen sie die gleiche Grösse besitzen wie die Randstacheln) kleiner als die Randstacheln; ihre Länge beträgt 0.048-0.060 mm, ihre Dicke 0.01-0.012 mm. Eine Hautbestachelung konnte ich bei keinem Exemplar nachweisen.

The contrast which Dietz describes in the spines of *E. revolutum* and *E. echinocephalum* is very slight when actually compared. That the corner spines are slightly smaller ($54\text{--}72\ \mu$, by $12\text{--}14\ \mu$ as compared with $48\text{--}60\ \mu$ by $10\text{--}12\ \mu$) than the others is really no contrast, for contrary to Dietz's statement it is the usual condition in *E. revolutum*. Dietz's figure "A" (see Pl. III, fig. 18) shows a very considerable addition to the difference given in his text. The measurements given in the text overlap both in length and width, and they are very near the mean length for the spines of *E. revolutum* at the same body size (Chart 6). If the distribution of the spines is as inaccurately figured as the size of the corner spines it can be assumed that no difference is shown in the cephalic spination in the two species. The figure shows a character that would distinguish *E. echinocephalum* but Dietz does not mention it. He has shown a distinct alternate arrangement in the lateral spines, a condition that does not occur in *E. revolutum*. If the figure could be accepted as reliable there would be no reason to discuss this species further for it could be distinguished from all of the other 37-spined forms of the genus by the character of these lateral spines. Since, however, as was shown above, the figure does not support the text and practically none of the written description actually disagrees with my own observations on specimens of *E. revolutum*, and furthermore, since only seven immature specimens were used for the description, and no one has since reported finding this species, it is very probable that *E. echinocephalum* is identical with *E. revolutum*. The measurements given by Dietz are added here since they do not agree in every detail with *E. revolutum*: oral sucker $90\text{--}120\ \mu$ in diameter; pharynx $100\text{--}120\ \mu$ by $80\text{--}110\ \mu$; acetabulum

0.37-0.44 mm in diameter. These measurements agree with corresponding ones for *E. revolutum* with the exception of the acetabulum, which is slightly larger than the same organ in unflattened specimens of *E. revolutum*. The figure given by Dietz (1910, Pl. X, fig. 4) appears slightly flattened although it is not so designated. Zunker (1925) re-examined the type material and confirmed Dietz's observations. His only significant remarks are that he could see no cuticular spination and that the acetabulum is large. Although I am not convinced that *E. echinocephalum* is distinct from *E. revolutum*, it is possible that it differs in the following characters: smooth cuticula, acetabulum four times larger than oral sucker while in *E. revolutum* it is only two to three times larger than the oral sucker in immature specimens. The six lateral spines are alternating instead of being unalternating, and the corner spines may be somewhat smaller in relation to the other cephalic spines.

Echinostoma miyagawai Ishii, 1932 (— *E. revolutum*).—This is a 37-spined form which Ishii (1932, pp. 91-100, Pl. 2, figs. 10, 11; Pl. 1, fig. 1) described from the domestic fowl and wild and domestic ducks in Japan. It is described as being 21-26 mm long by 2-3.5 mm wide. The head crown is 0.89-1.10 mm in diameter, and the 37 spines are arranged exactly as in *E. revolutum* in the figure. In the text, however, it is stated that six spines lie on each ventral side of the crown and the other 25 are arranged around the crown in two rows. It is clearly shown in the figure that only five spines occur on the ventral corners, the six laterals do not alternate, the fifteen remaining spines alternate across the dorsal side of the head, and the median spine is aboral as it is in *E. revolutum* (Figs. 22, 23). The figure also shows that the relative size of the spines is identical with *E. revolutum*. They are 84-108 μ in length and 26-28 μ in width, which also checks with *E. revolutum*. The oral sucker is 0.221-0.476 mm in diameter, the acetabulum is 0.714-1.088 mm and is 2.0-2.3 mm posterior to the oral sucker. The cuticular spines are closely set in the anterior part of the body but more scattered posteriorly. The diameter of the acetabulum is slightly less than the average for *E. revolutum* but is just within the range. The relative size of the two suckers is the same for the two forms and the diameter of the collar is also the same. The length of the pharynx is equal to the diameter of the oral sucker in both forms, and the internal organs of the two are identical throughout. Ishii says that his species resembles *Echinostoma cine-torchis* in body size and number of crown spines but differs from it in the character of the testes. Ishii's figures show the testes distinctly lobate while his figure of *E. revolutum* shows more rounded testes. It has already been pointed out that under some conditions the testes of *E. revolutum* are also lobate, more so than is shown in the figure for *E.*

miyagawai. Since there are no other characters, with the possible exception of the size of the acetabulum, by which to separate the two forms it seems very probable that they are identical. Ishii's *E. miyagawai* is merely a description of the very large specimens of *E. revolutum*. It is important to note that Ishii does not describe the individuals of his species that are less than 21 mm in length, and I am sure that a 10 mm specimen of "*E. miyagawai*" could not be distinguished from a 10 mm specimen of *E. revolutum*.*

Echinostoma cinetorchis Ando and Ozaki, 1923 (— *E. revolutum*).—*Echinostoma cinetorchis* is a 37-spined form which Ando and Ozaki found in the intestine of wild rats in Japan (Dollfus 1925, pp. 85-91, text figs. 1-3). It is a form that reaches a length of 21 mm and a corresponding width of 3.7 mm in flattened specimens. The oral sucker has a diameter of 0.26-0.30 mm in average specimens and 0.31-0.38 mm in the larger ones. The distance between the two suckers is 1.75-2.18 mm (about one-sixth of the body length) in average specimens and 2.29-2.95 mm (about one-ninth of the body length) in larger specimens. The acetabulum is 0.72-0.73 mm in diameter in average specimens and 1.01-1.18 mm in larger ones. Cuticular spination reaches the region of the posterior testis. The cephalic crown is 0.44-0.53 mm wide. The arrange-

*Two specimens and a communication from Ishii have been received since the above was written. The following notes are based on a study of them. Specimens 12.8 mm and 15 mm in length. Cuticula entirely lacking on both. On the smaller one there are thirty-seven cephalic spines arranged exactly as in *E. revolutum*; the relative size is typical and the actual size is near the average for specimens taken at delayed autopsy where they usually are shorter with points more blunt than the normal ones. The actual and relative size of the suckers, pharynx, and collar agree with *E. revolutum*. Vitellaria, uterus, ova, ovary, and cirrus also agree in general character, size and position. The testes, however, are more deeply lobed than any I have previously seen in this species, being constricted into four very definite lobes. The larger specimen has been fixed under considerable pressure and appears to have been dead in the host longer than does the smaller one. The cephalic spination does not differ from that in *E. revolutum* and as far as can be determined all other organs are identical with it. The testes are less deeply lobed than those in the smaller specimen but more so than is usually seen in *E. revolutum*. I have, however, several specimens in my collection with more deeply lobed testes, and I do not separate them from "sister" individuals on the basis of this character. In view of the fact that the cuticula is lacking on both specimens and the cephalic spines are rather blunt it seems evident that post-mortem changes must be taken into account here. The tissue's reaction to the stains support this view.

Through a personal communication Ishii has pointed out that he believes that *E. miyagawai* has a very long neck, longer esophagus, greater head crown, and longer crown spines than *E. revolutum*.

It is possible that a study of specimens that were fixed while still active would alter my conclusion, which is at present that the two are identical.

ment of the cephalic spines is the same as in *E. revolutum*. In average specimens the dorsal spines are 55-59 μ long by 11-13 μ wide. Those of the end groups are slightly smaller, 36-38 μ by 10-11 μ . The figure (see Fig. 15) of the crown shows that the relative size of the various spines is the same as for *E. revolutum*. The internal organs are apparently identical also. The egg size is 96-100 μ by 61-70 μ , which is about the same as for the largest specimens of *E. revolutum*. The testes are smooth or slightly lobed and are somewhat variable in position, the anterior testis being in some cases on the level with the ovary or even anterior to it. I have not observed any such extreme anomalies in my specimens of *E. revolutum*. Ando and Ozaki do not compare this form with *E. revolutum* or any of the other very numerous 37-spined species of the genus. Very extensive tabular comparisons of the descriptions and comparisons of every detail indicated in the figures fail to show a single difference in *E. cinetorchis* and *E. revolutum*. It is interesting and important to observe that both Ishii (1932) and Kurisu (1932) reported finding both species in the same region. The only assumption necessary to account for this, however, is that they have been misled by the very pronounced changes in body proportions that always occur in *E. revolutum* as its length increases over 12 mm.

Echinostoma armigerum Barker and Irvine, 1915 (— *E. revolutum*). —This is one of the four species of muskrat echinostomes described by Barker *et al* as having about 37 cephalic spines. Two of these species, *Echinoparyphium contiguum* and *Echinost. callawayensis*, have already been discussed. *Echinostoma armigerum* has been reported recently from the muskrat in Canada, and a brief description of it given by Law and Kennedy (1932, p. 24, fig. 15). Although both authors report it as common I have not been fortunate enough to obtain specimens for comparison with specimens in my own collection which seem to be identical with *E. armigerum* and are at the same time identical with *E. revolutum*. This form according to the original description (Barker, 1915, p. 189, text-fig. A) is 9.4 to 12.4 mm long by 1.2 to 1.8 mm wide. Cephalic spines 37 in number, 27 on the rim, and 5 on each ventral point of the collar. Collar spines 61 to 94 μ in length, and the ventral corner ones are the smaller. The anterior third of the body spiny. Uterine coils fairly compact in transverse coils. Eggs 84 to 105 μ by 57 to 66 μ . All other parts of the description would apply to almost any species of the genus. The figure (Barker's text-fig. A) so closely resembles a large number of the specimens in my own collection that I am convinced that they are identical and that Barker's *E. armigerum* is *E. revolutum* after it has reached a length of 9.4 to 12.4 mm. Comparison of the measurements for *E.*

revolutum and all points of description fail to show any difference in the two forms. *E. armigerum* is doubtless a synonym for *E. revolutum*.

Echinostoma coalitum Barker and C. A. Beaver, 1915 (— *E. revolutum*).—The fourth species of muskrat echinostome described by Barker is *E. coalitum*. It is also identical with *E. revolutum* and the same as *E. armigerum* but described from only the older and larger individuals. It is difficult to take muskrats alive and in most cases autopsies are made several hours post-mortem. The large specimens of *E. revolutum* die much sooner than the smaller ones and consequently most of the largest specimens in my collection were taken after the worms had died. I have, however, several specimens over 20 mm in length with firm bodies and good spination. The original description of *E. coalitum* was based upon "22 specimens of an unusually large trematode . . . found among several hundred specimens of different species of trematodes in the intestine of 46 muskrats." The body is described as "very flabby," which suggests that the specimens were dead when collected. They are 22 to 30 mm long by 1.5 to 2.3 mm wide at the level of the ovary. The anterior part of the body is covered with minute spines. The collar bears "35 spines arranged in a single or slightly alternate rows, 25 large spines on the rim and 5 smaller spines on each lappet." Oral sucker 0.37 to 0.46 mm in diameter. Acetabulum at the level of the second anterior sixth of the body, 1.12 to 1.32 mm in diameter. Uterus with dense transverse coils. Eggs numerous, 104 to 108 μ by 67 to 70 μ . When this form is compared with *E. revolutum* there is but one significant difference in the two. That is in the number of spines in the collar, there being only 35 instead of 37. There are, however, five on each corner lappet, and since most of the specimens studied were in all probability dead before fixation, there is a very strong probability that the 22 specimens studied did not show typical spination. Through the kindness of E. W. Price of the B. A. I. of the U. S. D. A., I have been able to study a slide (#30850) containing three specimens which were accessioned in the Washington collection under the name of *E. coalitum*. These specimens are 16 to 20 mm in length and identical with specimens which I have collected from the muskrat and have identified as *E. revolutum*. Although none of the three specimens on slide #30850 have a complete set of cephalic spines and all have lost the cuticular spination, it is evident from the pattern of the spines still present that they are the 37-spined *E. revolutum*. Law and Kennedy (1932, p. 16, fig. 9) report *E. coalitum* from the muskrat in Ontario, Canada. The description and figure given by them are about the same as Barker's. Leidy (1888, p. 126) also reported on an *Echinostoma* sp. from the muskrat. He had two collections, and in the

first one he says "there are 25 worms, and in their present condition they are pale brown bordered by dark brown, and measure from 12 to 18 mm long by 1 to 1.5 mm broad. If not identical, they are closely allied to *Distomum echinatum*, which in the mature state lives in ducks and other water birds and in the larval state in fresh-water snails. The muskrat eats the latter so that it may likewise become infested in the same manner as the ducks and this would also seem to make it probable that the parasite is the same." Leidy characterizes them as follows: 36 straight spines on the collar. Acetabulum much larger than the head, "situated at the base of the neck." The oral sucker is small and the pharynx oval. Body nearly the same width throughout. Testes almost midway between acetabulum and posterior end. Head 0.5 to 0.6 mm broad, spines about 100 by 20 μ , oral sucker 0.25 mm in diameter, pharynx 0.30 by 0.225 mm, and acetabulum 0.875 to 1.25 mm. Ova 100 by 72 μ . Regarding the second collection Leidy states: "Since the above communication a collection of worms, from the small intestine of a muskrat, has been received. Eighteen of the worms pertain to the supposed *Distomum echinatum*, and range from 18 to 25 mm long. In all, the fore part of the body a short distance behind the acetabulum is finely echinate, while the rest is smooth." Leidy did not report any observations on the cephalic spination of the second collection, but it is very probable that 37 instead of 36 spines could have been counted on these since they were, judging from the fact that the cuticular spination was intact, in a much better state of preservation than the first lot. Assuming that the spines on the first lot were atypical, the worms reported by Leidy can be considered correctly diagnosed by him as *Distomum echinatum* (= *Echinostoma revolutum*). It is perhaps important to note too that *Distomum echinatum* was at the time Leidy made this report sometimes characterized as having 36 rather than 37 cephalic spines.*

Echinostoma mendax Dietz, 1909 (= *E. revolutum*).—*Echinostoma mendax* is a 37-spined form that is so similar to *E. revolutum* that it has already been considered a doubtful species (Lutz, 1924, p. 81). Sprehn (1932, p. 306) lists it as a synonym of *E. revolutum* but does not indicate whether he has himself re-examined the types or not. It is obvious from the original description that it cannot be distinguished from *E. revolutum*. The only differences noted by Dietz himself are expressed in the following statements:

*Krull (1935) has recently made a brief report on a form which he has called *E. coalitum*. Since the morphology of the worm is not discussed, no confirmation of the above conclusion is given, although certain host records have been confirmed and certain others added (Tables 1, 2, and 3).

In der vordern Körperpartie ist die Cuticula sowohl auf der Dorsal—wie auf der Ventralseite mit feinen Hautstacheln besetzt, die sich jedoch im Gegensatz zu *Echinost. revolutum* auch in den Seitenrändern nicht über den Bauchsaugnapf nach hinten verfolgen lassen. . . . Der Bauchsaugnapf ist in Verhältnis zu *Echinost. revolutum* nur schwach entwickelt, kugelig (0.60-0.64 mm) oder ein wenig nach hinten verlängert (0.65-0.72 : 0.60-0.62 mm).

It has been shown that the cuticular spination varies with both the age of the worm and the type of host, and differences in it are unreliable for diagnosis (Chart 8). That there is a difference in the development of the acetabulum in the two forms is doubtful, for the measurements given by Dietz fall very near the average for *E. revolutum*. The figures given by Dietz (1910, text fig. A, Pl. 10, fig. 2) are identical in all the important diagnostic features with *E. revolutum*. In fact text figure A (see Pl. III, Fig. 16) shows very distinctly both the typical arrangement of the spines and the typical order in the relative lengths of the various spines. *Echinostoma mcndax* Dietz 1909 is without question identical with *Echinostoma revolutum*.

Echinostoma paraulum Dietz, 1909 (= *E. revolutum*), and *Echinostoma columbae* Zunker, 1925 (= *E. revolutum*).—*Echinostoma paraulum* was described by Dietz (1909, p. 300, Pl. 10, fig. 3, text-fig. B) from *Colymbus cristatus* and several species of ducks from middle Europe. Several authors (Baylis, 1929, p. 40; Iwata and Tamura, 1933, p. 2) have expressed strong doubts as to its legitimacy, while others (Skrjabin, 1915, p. 399; Sprehn, 1927, p. 454, 1930, p. 767, 1932, p. 314; Wetzel, 1933, p. 772) report its occurrence and consider it a valid species. Sprehn (1927, 1930, 1932) considers *E. columbae* Zunker 1925 a synonym of *E. paraulum*, and in 1930 he put it into the genus *Echinoparyphium*, although I am doubtful if this can be justified. The situation is made still more complex by the fact that *E. columbae* Zunker is variously described by Zunker (1925), Bolle (1925), Krause (1925a, b), Otte (1926), and Sprehn (1927, 1930, 1932). According to Dietz's original description *E. paraulum* is a form that ranges in length from 4 to 7 mm. Its other measurements are: greatest width 0.94 to 1.66 mm, width of head crown 0.43 to 0.54 mm, diameter of oral sucker and acetabulum, respectively 0.21 to 0.26 mm and 0.54 to 0.83 mm, pharynx 0.21 to 0.22 mm by 0.14 to 0.20 mm. The body is spiny as far posterior as the acetabulum on the dorsal side and to the testes on the ventral side. The 37 spines of the cephalic collar are arranged exactly as in *E. revolutum* and the relative size of the various spines is also identical with *E. revolutum* (Fig. 17). His figure of the entire worm is in all respects identical with a slightly contracted 6-7 mm specimen of *E. revolutum*. The middle constriction in the testes occurs not uncommonly in this species, particularly if the

specimen is either under pressure or fixed in the contracted condition. There is positively not a single character by which *E. paraulum* can be separated from *E. revolutum*.

Echinostoma columbae has been restudied by Sprehn and shown to be a synonym of *E. paraulum*, which probably is sufficient evidence that both *E. paraulum* and *E. columbae* are identical with *E. revolutum*. Since, however, the several descriptions of *E. columbae* differ, and especially since Sprehn (1930) has put this form into the genus *Echinoparyphium* a more complete study of the descriptions is necessary.

Krause (1925a) made a preliminary report on a number of pigeons infected with echinostomes of two species, a 37-spined form and one with forty-two spines. Then Zunker (1925) published a description of a 37-spined echinostome from the pigeon, which he considered closely related to *E. echinocephalum* but distinct from it. He called it *Echinostoma columbae* spec. nov. Then Krause (1925b) followed Zunker with a second report on his material. He described his specimens in good detail and considered it similar to *E. revolutum*, which it is indeed. Krause's description leaves no doubt in my mind that both his and Zunker's worms are *E. revolutum*. Zunker could find no cuticular spines on his worms, but Sprehn (1927) re-examined Zunker's worms and found them identical with a collection which he himself described as having a distinct cuticular spination over nearly all of the ventral side and the dorsal side of the anterior end. Bolle (1925) also corrected Zunker's observation regarding the cuticular spination. It was Bolle who first compared the pigeon echinostomes with *E. paraulum*, but he decided against their identity on the basis of differences in size of the crown spines and the position of the cirrus sac. Bolle described the dorsal spines of the head crown as being larger in the aboral row than in the oral. This feature prompted him to compare it with members of the genus *Echinoparyphium*. He could distinguish it from all members of that genus and decided that it was indeed a distinct species which should be designated as *Echinostoma columbae*. There is very little disagreement among the various authors that cannot be readily explained on the basis of differences in degree of maturity in the specimens studied by them. Zunker and Bolle both used smaller specimens while Krause and Sprehn had about average specimens. Sprehn emphasized the size difference in the spines of the two dorsal rows and observed (1927, p. 452) that "eine deutliche pars prostatica lässt sich in Schnitten nachweisen." He compared his specimens with the types for *E. paraulum* and found that they were identical. On the basis of these studies he declared all of the pigeon echinostomes with 37 cephalic spines to be

E. paraulum (= *E. columbae*). Krause, however, argued that these worms were most similar to *E. revolutum*. In spite of the fact that he had in a former communication declared that a pars prostatica was distinctly present in the worms studied by him, Sprehn (1930) offered the following reason for transferring them to the genus *Echinoparyphium*:

... bei ihm die Pars prostatica fehlt, die Hautbewaffnung die ganze Bauchseite überzieht und sich auch noch auf die Rückenseite ausdehnt und ausserdem ein doppelter Stachelkranz vorhanden ist. Bei den Arten der Gattung *Echinostoma* s. str. ist die Bestachelung dagegen nur auf die Bauchfläche des Vorderkörpers beschränkt und ausserdem eine Pars prostatica vorhanden.

That the two genera *Echinostoma* and *Echinoparyphium* cannot be separated on the basis of the cuticular spines is evident since all of the most recent researches on *E. revolutum* have shown that at least some dorsal cuticular spination is present. It is furthermore evident that Sprehn is in error in considering the crown spines of the pigeon echinostomes as more typical of the genus *Echinoparyphium*, for all of the figures given by himself (1927, fig. 1), Zunker (1925, fig. 2), and Bolle (1925, fig. 1) picture the head crown as being typical of *Echinostoma*, not *Echinoparyphium* (Figs. 19, 20, 21). They show a very slight size difference in the two rows, a condition characteristic of *E. revolutum* (Text-figs. 1, 2, 4, p. 24). The figures of both Bolle and Sprehn are drawn in a manner that emphasizes this difference, since the oral row is more vertical than the aboral, and spines thus seen in end view appear to be shorter. Were it not for the question of the pars prostatica, all of the pigeon echinostomes described by the above authors could be readily put into the genus *Echinostoma* s. str. and considered as unquestionable synonyms of *E. revolutum*. In 1927 Sprehn declared that in *Echinostoma paraulum* (= *E. columbae*) the pars prostatica is distinctly seen in sections. Three years later he contradicted his earlier statement and stated that "die Pars prostatica fehlt." The only figure of an entire specimen of one of these disputed forms is given by Zunker (1925, fig. 1). The length of the uterus alone prohibits putting it into the genus *Echinoparyphium* (Fig. 24). If this form can be distinguished from *E. revolutum* at all it is on the basis of Sprehn's later statement that the pars prostatica is absent.

Van Heelsbergen (1927) and Picard (1930) have also reported finding echinostomes in pigeons, but neither has made a final identification of his material. The figures and data given by them suggest that each found both *E. revolutum* and *Echinop. recurvatum*.

MISDETERMINATIONS.—In addition to the large number of doubtful species and synonyms there are a few obvious misdeterminations that should be mentioned. Looss (1899, p. 681) has already called attention

to the misdetermination by Wedl (1857, pp. 245-246, Pl. 1, figs. 5-6). Wedl's form which was taken from *Phalacrocorax carbo* is not even closely related to *Echinostoma revolutum*. A form which Ercolani (1881, 1882) determined as *E. echinatum* obviously does not belong to the genus *Echinostoma* s. str. His figures (1881, Pl. 1, figs. 50-58, Pl. 2, figs. 1-5; 1882, Pl. 3, figs. 19-21) were copied by Railliet (1895, fig. 244) and designated as *D. hérissé* (*D. echinatum* Zeder). Neumann (Neumann-MacQueen, 1905, fig. 237) also copied these figures and put them under the name *Echinostomum echinatum*.

Johnson (1920, p. 368) has doubted Looss' determination of a form which he found in *Machetes pugnax* (1899, pp. 683-684, Pl. 24, figs. 6, 7). Looss described it as a variation of *Echinostoma revolutum*. Several of the crown spines had been lost but the exact point where some of them had been could be located, so that a total of 34 spines was accounted for. Since this form did not differ in other respects from the *E. revolutum* of other hosts Looss did not make a new species of it. Johnson was of the opinion that the host in this case was so different from the "normal" that it might be expected to be a new species of worm. He argued also that the spination in the two forms (those from ducks and those from *M. pugnax*) is very different, a point on which I cannot agree with him. The fact that only 34 spines are shown does not mean that the form is a 34-spined species. Looss made it clear in the text that the spines were not all present and that only 29 were actually observed. The difference in the size range in the eggs was also a point in Johnson's argument, but this is not, in my opinion, significant, since the measurements given by Looss (101 to 110 μ by 59 to 63 μ) are easily within the range for *E. revolutum*. Taking all of these facts into consideration there can be little doubt that Looss has correctly identified his material and that *Echinostoma limicoli*, the name which Johnson suggested for Looss' worm, is a synonym of *E. revolutum* (cf. Figs. 28, 29).

Looss' figure of the metacercaria of *E. echinatum* (1894, Pl. 9, fig. 192) is, on the other hand, a misdetermination. Sewell (1922, p. 122) has suggested that Looss' figure (1894, fig. 191) of the cercaria is also a misdetermination because of the difference in the excretory system of it and the young adult. Judging solely on the basis of the cephalic spination there can be no doubt that the figure of the metacercaria is not that of *E. revolutum*. It is instead very similar to *Echinoparyphium aconiatum* Dietz, a form which also has 37 spines. The corner spines in Looss' figures are four in number, all nearly equal and very much larger than the other crown spines. These characters are present in *Echinop. aconiatum* but not in *Echinost. revolutum*.

SUMMARY OF FORMS DISCUSSED.—The present status of the forms discussed and the conclusions the present study has led to may be summarized as follows: *Echinostoma revolutum* can be distinguished from all other described forms by the following characters: (1) 37 cephalic spines arranged in the manner indicated by $(3 + 2) + 6 + (7 + 8) + 6 + (3 + 2)$, which means that there are 5 on each ventral lappet, 3 of which are on the surface or oral in position and 2 deeper in the flesh or aboral, 6 unalternating laterals, 15 dorsals arranged in alternating fashion with 8 orals and 7 aborals. The median spine is in the aboral row which is continuous with the row containing the six lateral spines. (2) The ventral side of the body is spiny as far back as the anterior testis or farther, and the dorsal side bears spines in most specimens but may be without them in older worms from bird hosts. (3) The uterus is long, containing eight or more coils even in the smallest mature worms. (4) The proportions of the body change with age as indicated in Charts 1-7.

Echinoparyphium aconiatum and *Echinoparyphium contiguum* are distinguished from *Echinostoma revolutum* by the very short uterus and the different arrangement of the cephalic spines, *Echinop. aconiatum* having an arrangement that is different in all parts of the crown. *Echinoparyphium contiguum* must be redescribed before it can be definitely separated from *Echinop. aconiatum*. None of the other species discussed can be positively separated from *Echinostoma revolutum*. It may seem almost incredible that all sixteen of the species discussed here must be either reduced to synonymy or considered as doubtful species. It may also seem that too much emphasis has been placed on the similarity of the cephalic spination, and too little attention given to other structures. In most cases the character of the cephalic spination has borne more weight in my decisions than any other one factor. It must be conceded, however, that it is highly improbable that any two species could be identical in number, arrangement, and relative size of these 37 structures and at the same time be sufficiently dissimilar in other respects to be recognized as separate species. *Echinostoma miyagawai*, *cinetorchis*, *armigerum*, *mendax*, *paraulum*, and *columbae* are all unquestionably identical in this respect, and more than sufficient evidence is at hand to prove beyond reasonable doubt that the other two species which have been declared synonyms are indeed identical. Insufficient information regarding variations due to the age and the host as well as the question of host specificity account in part at least for the rather long list of synonyms. The procedure recommended by Kowalewski (1897) for designating synonyms is followed in the summary below:

Echinostoma revolutum (Froelich, 1802)

Syn. dem.

- (Dietz, 1910) *Distomum echinatum* Zeder, 1803
 (P. Beaver, present paper) *Echinostoma miyagawai* Ishii, 1932
 (Idem) *Echinostoma cinetorchis* Ando and Ozaki, 1923
 (Idem) *Echinostoma armigerum* Barker and Irvine, 1915
 (Idem) *Echinostoma coalitum* Barker and C. A. Beaver, 1915
 (Lutz, 1924; Sprehn, 1932; P. Beaver, present paper) *Echinostoma mendax* Dietz, 1909.
 (Baylis, 1929; Iwata and Tamura, 1933; P. Beaver, present paper) *Echinostoma paraulum* Dietz, 1909.
 (Krause, 1925a, b; P. Beaver, present paper) *Echinostoma columbae* Zunker, 1925.
 (P. Beaver, present paper) *Echinostoma limicoli* Johnson, 1920.

Syn. inq.

- Echinostoma sudanense* Odhner, 1911
Echinostoma acuticauda Nicoll, 1914
Echinostoma callawayensis Barker and Noll, 1915
Echinostoma erraticum Lutz, 1924
Echinostoma neglectum Lutz, 1924
Echinostoma nephrocystis Lutz, 1924
Echinostoma microrchis Lutz, 1924
Echinostoma echinocephalum (Rud., 1819)
Echinostoma oxycephalum (Rud., 1819)
Echinostoma dilatatum (Miram, 1840)
Echinostoma armatum (Molin, 1850)

PROTOCOL OF EXPERIMENTS

ON THE DETERMINATION OF METHODS, PURITY OF
STOCKS, AND HOSTS

Preliminary experiments had shown that by feeding the cysts of the 37-spined echinostome cercariae to various birds and mammals, 37-spined adults could be recovered from them. This was not always true, however, as sometimes a negative was obtained even though it was definitely known that an abundance of cysts had been fed. This was particularly true with rats; and in one case a negative was obtained from a pigeon although it is probable that the snail fed did not contain cysts. With these experiences unexplained and Tubangui's (1932b) somewhat similar experience with pigeons and rats in mind it seemed possible that more than a single species or at least two varieties of the same species were being handled. Careful examination of the cercariae from each of the infected snails collected in various localities failed to disclose, however, what could be considered more than one species with 37 spines. Since several echinostome species have been described as having 37 cephalic spines, it was thought imperative to check the purity of the material employed.

The experiments to check on the above question are as follows: infected snails (*H. trivolvis*) were collected from three different localities (Table 8, p. 77), which represent three different streams and two entirely separate drainage systems, although only about thirty miles separate the headwaters of one from the other at the nearest point. The snails were wiped dry as they were collected in the field so that no cercariae could emerge and become mixed. Then as soon as they were brought into the laboratory each of them was cleaned, marked with india ink, and registered before they were isolated in various clear glass containers, usually eight-dram vials. Special care was employed to guarantee that no cercariae escaping from one snail might be allowed to mix with those of another. At no time during the experiments were any two infected snails in the same container. As soon as cercariae emerged they were examined to check on the various morphological characters used in diagnosis of species, especially the number, distribution, and relative size of the cephalic spines; body spination; character of the tail fin; number of cephalic ducts; and the main ducts of the excretory system. Size was also checked. In every case the characters exhibited were apparently identical. After the cercariae were checked the snail was given an additional number and again registered, so that complete records were kept on each infected snail. Various secondary intermediate hosts of laboratory origin were employed: *Physa gyrina*, *Helisoma trivolvis*, and tadpoles. Usually *Physa* were used. No careful check was kept on the number of cysts fed as this was thought to consume too much time to be worth while in this particular series of experiments. The following is a brief outline of the separate feedings and results. The experiments carry the same designation as the registered number of the snails which produced the cercariae, in addition to "1, 2, 3," etc. A single snail produced all of the cercariae used in each experiment. For example, in experiment 1, snail C3-A was used; in experiment 2, C4-28; etc.

EXPERIMENT 1(C3-A)

On 7/28/33 Pigeon 7 was fed two small *Physa* carrying many C3-A cysts, 1 day to 2 weeks old. Ten days later this pigeon developed a severe bloody diarrhea which continued into the next day. No ova were present yet in the stools when it was killed and examined on 8/8. The examination was made immediately, and 621 worms were recovered, none of which were really mature although about 30% of them had 5-20 ova in the lower uterus. These worms were scattered along the gut from anus to proventriculus. There were 44 worms in the gizzard but over half of these were dead. Most of the worms were in the lower duodenum and upper ileum. It is also of interest to note that two active worms were taken from above the gall bladder in the liver and nine were in the oviduct (upper). Death appeared to be imminent at the time the host was killed.

On 8/13/33 a half-grown albino rabbit (Rabbit 2) was fed three small *Physa* carrying many C3-A cysts, 1-14 days old. This animal died on 8/17. The autopsy was made 6-8 hours post-mortem and 284 specimens were recovered from about the middle of the ileum. Whether the worms were responsible for the death of this host is uncertain. It developed a rather severe diarrhea 36 hours before death, which may have been due to a change from a dry to a green diet. As all the other rabbits procured at the same time were fed infective cysts and as they too died, there was no control animal.

EXPERIMENT 2(C4-28)

Pigeon 10 was fed one small *Physa* with cysts on 8/13/33. Ova appeared in the feces on 8/22 and were more numerous each day until 8/26 when it was killed and 18 mature worms were taken from the middle ileum.

Rabbit 4, a half-grown albino, was fed 2 *Physa* with numerous cysts on 8/13/33. It died on 8/20 and was autopsied 3-4 hours post-mortem. One hundred twenty-two immature worms were taken from the ileum, for the most part from the second and third twelve inches above the cecum. It is uncertain as to whether or not the worms caused the host's death.

EXPERIMENT 3(C4-16)

Rabbit 5 was fed 2 *Physa*, each with about 100 cysts, on 8/31/33. Ova appeared in the feces on 9/12 and became more numerous daily until 9/17 when the host was killed and 28 mature worms taken from the lower and middle ileum.

Rabbit 6 was supposedly fed 1 *Physa* on 8/31. It fought violently, however, and it was thought doubtful at the time that any part of the snail was actually swallowed. It was not surprising then that its feces were negative, and no worms were found when it was killed on 9/18.

Pigeon 11 was fed 2 small *Physa* on 8/31/33. Ova appeared in the feces on 9/12 but were not numerous. They were easily found, however, by direct examination for five days, but none were found on the sixth. The pigeon was then killed and no worms were found.

EXPERIMENT 4(C5-A)

Pigeon 9, Rabbit 3, and Dog 1 were used in this experiment.

Pigeon 9 was fed 2 *Physa* with many C5-A cysts one to seven days old on 8/13/33. A few ova appeared in the feces on 8/22, were fairly numerous the next day, and very numerous on 8/24 when the pigeon was killed and 580 worms recovered. Some of those from the upper ileum were immature.

Rabbit 3 was fed C5-A cysts in one medium-sized *Physa* on 8/13/33. This rabbit died on 8/21/33 before the worms matured. The autopsy was made 12-14 hours post-mortem and 540 worms were recovered from the ileum, most of them about half-way between the duodenum and cecum. Many of those near the upper and lower ends were dead.

Dog 1 was fed C5-A cysts in 3 small *Physa* on 8/31/33. It was killed on 9/18 and 7 slightly immature worms were taken from the cecum and just above it in the lower ileum.

EXPERIMENT 5(C6-2)

Chicken 5, Dog 3, Cat 5, and Rats 30 and 31 were given cysts of C6-2.

Chicken 5 was fed a small *Helisoma* containing relatively few cysts on

9/19/33. On 10/1 the feces became positive for ova and on the next day the ova were abundant. The host was killed on 10/2 and 46 worms were taken from the middle ileum.

Dog 3, a setter bitch pup, was given 3 small Physa each harboring about 25 cysts and a tadpole with an unknown number of cysts on 9/15/33. This dog was anesthetized on 9/26 and devocalized, a procedure which caused an illness of about one week. Afterwards, however, it maintained good health and was found by fecal examination on 10/8 to be infected. It was then killed and 64 mature worms recovered from the second and third twelve inches of the ileum above the cecum.

Cat 5 was fed about 200 cysts in 6 very small Physa on 9/24/33. This cat was only about one-fourth grown and in rather poor health when given the cysts. It ate a normal meal of bread and milk at the time the cysts were given but refused to eat afterwards. It was passing a little blood in frequent stools the next day and soon developed a severe bloody diarrhea and died just 48 hours after it had eaten the cysts. Autopsy was delayed 12-14 hours, and was not thoroughly done. Only three specimens were discovered and these were badly disintegrated.

Rats 30 and 31 were fed 7 crushed Physa containing many metacercariae on 9/27/33. No ova were discovered in the feces, and when they were killed on 10/18 no worms were found.

EXPERIMENT 6 (C6-3)

Chicken 6, Cat 2, and Pigeon 19 were fed the metacercariae of C6-3.

Chicken 6 was given 4 small Physa, each with a few cysts, on 9/19/33. Ova were found in the feces on 10/1 but were never numerous. Only two specimens were present when the host was examined on 10/5 and these were both in the cloaca.

Cat 2 was fed numerous metacercariae in a tadpole and one Helisoma. It became ill soon afterwards and on 10/2 looked as though it soon would die. The next day it was found in a state of coma. It was then killed and 39 immature worms taken from the lower ileum, 13 of which were dead. As the autopsy was made immediately it is certain that the worms were dead even before the host was killed.

Pigeon 19 was fed metacercariae on 9/27/33 in 4 small Physa. Ova appeared in the feces on 10/9 and nine days later the animal was killed. There were 93 worms in the middle ileum. This pigeon was also heavily parasitized with an internal mite.

EXPERIMENT 7 (C6-5)

Rabbit 8, Pigeon 16, and Mice 14, 15, 16, and 17 were fed metacercariae of C6-5. They developed in the rabbit and pigeon but the mice were negative.

Rabbit 8 was fed metacercariae in a tadpole (*R. pipiens*) and 2 small Physa on 9/15/33. Ova were found in the feces on 9/27 and increased daily until the animal was killed (10/2). There were five mature worms in the middle ileum.

The four mice were fed five small Physa with metacercariae on 9/14/33. They were all negative when examined on 9/29.

Pigeon 16 was fed metacercariae in four small Physa on 9/28/33. The cysts were 1-7 days old. Ova did not appear until 10/12, several days later than was expected. It was killed on 10/13 and found heavily parasitized. There were 291 of the worms and about 1000 internal mites in addition. This may account for the delayed appearance of the ova. The 291 worms were scattered from lower ileum to duodenum, but most of them were in the middle section.

EXPERIMENT 8(C6-6)

Chicken 7, Guinea pig 1, and Rats 25 and 26 were fed metacercariae of C6-6. The chicken, guinea pig, and Rat 26 were positive but no worms were found in Rat 25.

Chicken 7 was fed metacercariae in 2 Physa on 9/19/33. It was killed on 9/30 in order to get some immature worms for another experiment. Only one worm was present, however. It was located in the lower ileum about ten inches above the ceca.

Guinea pig 1 was given a medium-sized *Helisoma* on 9/20/33 which had been in a finger bowl with the snail for about one week. It ate well and maintained good health until 9/30 when it became restless and refused food. The next morning it was dead. Autopsy was made about six hours post-mortem and the immediate cause of its death was found to be a large perforated duodenal ulcer. As there were 354 worms recovered from this host and nearly half of them were almost mature it seems very probable that they were in part at least responsible for the host's death. They were rather unevenly distributed between the middle colon and the stomach.

Rat 25 had been fed metacercariae from another snail (C6-10) on 9/15/33 but as it was never positive by fecal examination it was not killed. Then on 10/15 it was given a medium sized *Physa* carrying about 100 C6-6 metacercariae. The stools were never positive but as the feces were always solid it was thought that worms were possibly present even though no ova could be found. No worms were found, however, when it was killed on 11/4.

Rat 26 had been fed C6-11 metacercariae on 9/15/33 and although they must have been present no ova had been found in the feces up to 10/12. The pellets were always dry enough to collapse the ova and thus render the examination very difficult. A soft pellet was examined on 10/24, only twelve days after it had been fed C6-6 metacercariae and ova were easily found. This rat had been fed 26 or more metacercariae teased out of the kidneys of a tadpole (*R. pipiens*). These cysts were administered by mixing them into a bit of cornmeal and water. On 10/24 there were 33 worms in the middle ileum, three of which were much larger than the others and had the uterus well distended with ova. These were doubtless C6-11, which were fed on 9/15, and the other 30 were the C6-6. As was noted above, 26 metacercariae were counted in the kidney tissue, but several others could have been present but obscured from view.

EXPERIMENT 9(C6-7)

Rabbit 7, Chicken 3, and Pigeon 17 were used in this experiment. Worms developed in all three.

Rabbit 7 was fed 4 small *Physa* on 9/15 which carried metacercariae less than four days old. It was found positive by fecal examination on 9/27 and was killed six days later. There were 29 worms recovered, mostly from the middle ileum.

Chicken 3 was fed metacercariae in 3 small *Physa* on 9/19. A few ova were found in the feces on 10/1, and they were somewhat more numerous the next day when the animal was killed. Autopsy was made three hours post-mortem and 22 worms recovered. Most of them were in the middle ileum.

Pigeon 17 was given metacercariae in 7 small *Physa* on 9/28/33. A few ova were found on 10/9 and 10/11. It was killed on 10/11 and only two specimens were present, one of them not quite mature. They were in the middle ileum.

EXPERIMENT 10(C6-8)

Duck 3, Cat 4, and Pigeon 18 were fed metacercariae from C6-8. The cat and pigeon were positive; the duck was negative.

Duck 3 was fed 3 Physa carrying very many metacercariae on 9/15. No fecal examinations were made and when it was killed on 9/23 no worms were present. Although two or more explanations may be made for this the most probable is that the host was allowed to go without food for about a week. This occurred by accident, not as a part of the experiment.

Cat 4 was fed a Helisoma and 7 small Physa, each carrying a few metacercariae, on 9/23/33. Ova appeared in the feces on 10/13/33 and were found in abundance the following day. On 10/14 the host was killed and 352 worms taken from the caudal three feet of the ileum; 297 of these were concentrated into the second foot above the cecum.

Pigeon 18 was fed metacercariae on 9/28/33 in 2 small Physa. The feces became positive for ova on 10/9 and three days later the host was killed. The autopsy was delayed three hours. There were 80 worms entangled in the feathers around the anus, 74 in the cloaca and rectum, and 41 in the caudal four inches of the ileum.

EXPERIMENT 11(C6-9)

Pigeon 15 and Rat 27 were fed metacercariae of C6-9 and worms developed in both of them.

Pigeon 15 was fed the metacercariae in 2 small Physa on 9/15/33. Positive stools were passed on 9/27. Two days later it was killed and 63 worms taken from the middle ileum.

Rat 27 was fed a single tadpole (*R. pipiens*) that had been in four ounces of water with snail C6-9 during the 36 hours which immediately preceded the feeding on 9/15/33. Thus the cysts were 1-36 hours old. This host was killed by another rat on 9/29. The autopsy was made about ten hours post-mortem. There were 431 worms in the ileum, most of them near the middle. It is important to note that these 431 worms all developed from the metacercariae in one frog larva. It is also of importance to note that none of the cysts were over 36 hours old when administered.

EXPERIMENT 12(C6-11)

Hog 2, Pigeon 13, and Rat 26 were fed metacercariae of C6-11. The worms developed in all three.

Hog 2 was fed the cysts in 4 small Physa on 9/14/33. On 9/26 it was slaughtered and the autopsy made fourteen hours post-mortem. There were 32 worms recovered from the caudal eight feet of the ileum. Ten of these worms were dead and all were immature.

Pigeon 13 was given metacercariae in 2 small Physa on 9/15/33. Ova were found in the feces on 9/27, but may have been present earlier as no examination was made previous to that date. It was killed and 31 worms recovered on 9/30. Most of them were in the middle ileum.

Rat 26 was fed metacercariae in one tadpole on 9/15/33. It was killed on 10/24 and 3 large worms recovered from the middle ileum.

EXPERIMENT 13(C6-12)

Hog 3 and Pigeon 14 were fed metacercariae of C6-12. Both were positive.

Hog 3 was given the metacercariae in 5 small Physa on 9/14/33. No fecal

examinations were made. On 10/16 the animal was slaughtered and eight mature worms were recovered from the caudal one-fifth of the ileum, the most posterior one being about eighteen inches above the cecum. The autopsy was made about three hours post-mortem.

Pigeon 14 was given the metacercariae in 2 small *Physa* on 10/5/33. Ova appeared in the feces on 10/15 and were numerous for four days, then suddenly decreased and no more were found after the fifth day. The host was not killed.

EXPERIMENT 14(C6-17)

Rat 28 and Chicken 4 were fed metacercariae of C6-17 and worms developed in both of them.

Rat 28 was fed the metacercariae on 9/18/33 in one small tadpole (*R. pipiens*) that had been dead about eighteen hours. This rat seemed normal in every way until 10/2 when it was noticed that it had not eaten on that day. The next day it was obviously very ill. It was killed and an autopsy performed immediately. Ninety-five worms were taken from the middle and upper ileum. Some of them had ova in the uterus.

Chicken 4 was fed metacercariae in 2 small *Physa* on 9/19/33. Ova appeared in the feces on 10/1, and increased in abundance daily. On 10/4 the host was killed and 30 mature worms taken from the cloaca, rectum, ceca, and ileum. The autopsy was made about one hour post-mortem.

A summary of the above experimental feedings is given in Table 5. In all fourteen of the experimental feedings in which both birds and mammals were fed encysted cercariae from the same snail host, there is no instance of failure to infect at least one of each. Some of the hosts were entirely negative and others lost their infection before they were killed. Results with the rats were particularly inconsistent and somewhat confusing. Several races of rats were used, however, and there is a very great difference in the way each serves as a host for this species of worm (Table 6). Mature worms of each of the stocks were not always procured from more than one host, but there are, it seems, more than enough cases, nine in all, in which mature worms were recovered in considerable numbers from both birds and mammals to show that only one species was used in infecting both types of hosts. As was indicated above, there are not enough morphological differences in any of the cercariae used even to suggest a mixture of species, and the morphological variation in the adults is interpreted as being induced by the different host species (see p. 27).

ON THE TRANSFER OF ADULT WORMS FROM HOST TO HOST

In order to test further the possibility of physiologic differences in the worms from the different hosts a number of experiments were undertaken in which identical worms rather than worms of common parentage were used. Worms taken from mammals and introduced into the cloaca of pigeons were able to adjust themselves to the higher temperature, more

active gut, etc., and generate large numbers of ova for from several days to several weeks (Tables 7 and 9, p. 77). The individual transfers were made as described below. Some of them were bird-to-bird transfers which gave data on questions other than the one mentioned above.

TRANSFER I

Six mature worms (13 days old) were transferred from the lower ileum of Chicken 5 into the cloaca of Pigeon T1 at 9 A.M., 10/2/33. This pigeon like most of the others was put in a cage over a shallow pan of water for a day or two in order to check whether the worms were immediately expelled. None had been expelled after 24 hours. Ova appeared immediately in the feces and were very numerous the next day. There was no apparent reduction in the numbers until after twelve days (10/16) when there was a rather sharp decline. During the next ten days there was no further decline. On 10/27 the eggs were scarce and none were found after 10/28. At least one of the original six worms lived 26 days in the new host.

TRANSFER II

Six mature worms, 18 days old, were taken from the middle ileum of Rabbit 7 and transferred to the cloaca of Pigeon T2 on 10/3. Two hours later one of the worms was discovered in the pan under the cage. None others were found 24 hours later, however, so it was considered that five worms were successfully introduced. Ova appeared immediately and were numerous for five days. None were found after the sixth day (10/9).

TRANSFER III

Ten mature worms, 23 days old, were taken from the lower ileum of Dog 3 and transferred to the cloaca of Pigeon T3 on 10/8. Seven were expelled as soon as the pigeon was released but when they were reintroduced they established themselves successfully. Ova were found in very great abundance until 10/27 when there was a noticeable decline. A gradual decrease followed and none were found after 11/2.

TRANSFER IV

The pigeon used in Transfer II was also used in this one. It was given ten mature worms from the upper ileum of Pigeon 18 on 10/12. The worms were 14 days old. Ova were found daily until 10/25. They were never very numerous, however. It is important to note that this pigeon had only three days previous to this transfer lost the last of the worms from Transfer II.

TRANSFER V

This transfer was made from the upper ileum of Pigeon 19 to the cloaca of Pigeon T5 on 10/18. Only one robust worm was transferred. It was then 21 days old. Ova were found in very great abundance, 3,000 per 24 hours on 10/22. On 11/26 this worm was producing only 700 per 24 hours, and on 11/28 none could be found.

TRANSFER VI

A transfer was made from the middle ileum of Rat 26 to Pigeon T6. A single mature worm 39 days old was used. The pigeon had been used as Pigeon 14,

which had been infected from stock C6-12 and has lost its infection after fifteen days (10/20). The transfer was made on 10/24. Ova appeared in the feces immediately and continued for six days only.

TRANSFER VII

A single specimen, age 12 days, was taken from the middle ileum of Rat 26 and introduced into Pigeon T7. This pigeon had never been infected before. Ova did not appear until the fifth day after the transfer and continued for about two weeks. The last positive stool was found on 11/14.

TRANSFER VIII

Same as Transfer VII. Pigeon T8 had never been used in previous experiments. Ova appeared in the feces on the fifth day and continued three days longer than in T7. The last positive stool was found on 11/17.

TRANSFER IX

Like the above. Pigeon T9 lost its worm, however, before it matured.

TRANSFER X

Similar to VII, VIII, and IX. Pigeon T10 had never been infected before. The ova appeared on the fifth day and continued five days longer than in T8 and eight days longer than in T7. The last positive stool was found on 11/22, on the 28th day after the transfer.

A summary of these experiments is given in Table 9.

From the above experiments in which metacercariae of common parentage were fed to several hosts including in most cases both birds and mammals, and in the experiments in which worms were transferred from one host to another, the conclusions that may be reached are: (1) that the experimental worms constitute but a single species which (2) demonstrates a very high degree of adaptability, being able even after maturity is reached, to adjust itself to a new host that is very different from the original, thus (3) inter-class transfers are easily made, and (4) it is also probable that the life of the worms is prolonged somewhat by the transfer, which suggests that (5) there is probably a slight immunity developed which is of an accumulative nature. These points are discussed at length in the text (pp. 18-33).

CONCLUSIONS

When the previous studies on the life history and individual stages of the cycle were restudied it was found that relatively few of the older researches could be definitely shown to pertain to *Echinostoma revolutum*.

The eggs of this species hatch in about three weeks into miracidia which penetrate any one of a great variety of pulmonate snails and prob-

ably metamorphose into sporocysts which produce mother rediae which in turn produce a second generation of rediae. These daughter rediae produce cercariae which begin to emerge in about three months.

The cercaria resembles the adult so closely in cephalic spination that positive identifications can be made from this character alone. Other features by which it can be recognized are the tail-fin membrane and the twelve cephalic ducts and gland cells arranged in two groups. The arrangement of the units of the excretory system may also aid in identification.

In addition to the descriptions of cercariae that have been identified as *Cercaria Echinostomi-revoluti* by feeding experiments there are eleven other descriptions of 37-spined cercariae in the more recent literature. These cercariae are easily separated into two types and perhaps only two species. At least only two species of the 37-spined cercariae can be positively recognized.

Cercaria helvetica xxiv Dubois and *Cercaria trivolvis* Cort are synonyms of *Cercaria Echinostomi-revoluti*.

It is shown by this study that the cephalic spination is the most reliable character for diagnosis of the adult worm. The arrangement and relative size of the cephalic spines distinguish it from the other 37-spined echinostomes.

The morphology of the adult worm is best described by the use of graphs which describe any given size from the entire range of from 2 to over 20 mm in length.

The only character that is not variable with age is the number, arrangement, and relative size of the cephalic spines.

By transferring single individuals from one host to another it was found that individuals of this species produce as many as 4,600 ova per day. The same experiments have shown that self-fertilization is possible and that it does occur when the possibility of cross-fertilization is precluded.

A study of the original and other earlier descriptions of *E. revolutum* have shown that none of these records and descriptions can be accepted without so much reservation as to render them almost valueless.

Eighteen species of adult echinostomes have been described more recently as having about 37 cephalic spines. Two of them belong to the genus *Echinoparyphium* and are easily distinguished from *Echinostoma revolutum*. None of the other forms can be positively distinguished from one another or from *E. revolutum*. In addition to *Echinostoma echinatum*, which has already been reduced to synonymy, eight others are shown to be synonyms and eight are shown to be probable synonyms or species of dubious standing.

Echinostoma revolutum has been found in the temperate zone of all parts of the world excepting South Africa and the interior of Asia. The cercaria is recorded from eleven species of pulmonate snails in diverse geographical regions. The metacercaria may be found in molluscs, amphibia, fish, and (?) planaria. It is recorded from sixteen molluscs, primarily pulmonate gastropods; probably eight species of amphibia; and one scaleless fish, *Ameirus melas*. The adult worm is recorded from 32 species of birds and nine species of mammals, including man. The present study has contributed ten new records for the metacercaria and seventeen for the adult.

It is shown that experimental and "incidental" hosts are "normal" if not natural hosts for this species of parasite and that natural infection would probably occur in almost any bird or mammal whose feeding habits are similar to the so-called "natural" hosts.

By repeatedly infecting both tadpoles and snails from the same stock of cercariae and feeding these to both birds and mammals it was shown that only one species of parasite was being studied rather than two or more indistinguishable forms, and that there is relatively no specificity shown in the metacercaria and adult stages.

Experiments in which worms were transferred from mammals to birds support the above conclusions.

The same transfer experiments indicate that the life of the parasite is prolonged by introduction into a new host.

Transfer and reinfection experiments have demonstrated that although prolonged captivity of the host and unsuitable diet produce more obvious reactions which tend to obscure immunity phenomena, the pigeon does develop a slight immunity to *E. revolutum*.

A total of 42 different measurements on each of about 300 worms were made and the worms from birds compared by biometric methods with those from mammals. While the differences are in most respects slight they are nevertheless in many instances significant, and may account for a good deal of the confusion regarding the morphology of the adult worm. The most obvious differences were found in the character of the cuticular spination. Differences in proportions are probably due to the very pronounced difference in growth rate in the two types of hosts.

SUMMARY

The life history of the trematode parasite *Echinostoma revolutum* has been experimentally determined and the morphology of the various stages described.

The adult worm has been described by biometric methods, which was found to be the only adequate means of description for a worm whose size range in adult life is so great as to allow much confusion in diagnosis.

Extensive studies have been made on normal variation, especially the variation induced by the different types of hosts.

Related species have been reviewed and eight species reduced to synonymy.

All of the more reliable records of hosts and distribution have been reviewed and summarized.

For the first time adult worms have been successfully transferred from mammal- to bird-hosts.

Certain immunity phenomena have been observed and discussed.

TABLE 1.—*Cercaria Echinostomi revoluti*
(e = experimental infection only)

Host	Locality	Reference
<i>Helisoma trivolvis</i>	Illinois Illinois Illinois Ontario	Cort, 1914, 1915 Faust, 1918 Beaver (this paper) Fallis, 1934
<i>Lymnaea peregra</i> .	Philippine Islands	Tubangui, 1932b
<i>Lymnaea pervia</i> .	Taiwan Taiwan	Tsuchimochi, 1924 Morishita, 1929
<i>Lymnaea radix</i>	Taiwan	Tsuchimochi, 1924, 1926
<i>Lymnaea stagnalis</i>	Italy Switzerland	Vevers, 1923 Dubois, 1928
<i>Lymnaea swinhoe</i>	Taiwan	Tsuchimochi, 1924
<i>Physa gyrina</i>	Illinois Ontario	E. L. Miller, 1936 Fallis, 1934
<i>Physa occidentalis</i> (?)	California	Johnson, 1920
<i>Physa rivalis</i>	Brazil	Lutz, 1924
<i>Planorbis</i> sp.	Taiwan	Tsuchimochi, 1924 1926
<i>Pseudosuccinea columella</i> . .	Maryland	Krull, 1935 (e)
<i>Stagnicola palustris</i>	Ontario	Fallis, 1934

TABLE 2.—*Metacercaria Echinostomi revoluti*
(e = experimental infection only)

Host	Locality	Reference
<i>Corbicula producta</i>	Taiwan	Anazawa, 1929
<i>Fossaria abrusa</i>	Ontario	Fallis, 1934
<i>Fossaria modicella</i>	Illinois Ontario	Beaver (this paper) (e) Fallis, 1934
<i>Helisoma trivolvis</i>	Illinois Ontario Maryland	Beaver (this paper) Fallis, 1934 Krull, 1935 (e)
<i>Lymnaea peregra</i>	Philippine Islands	Tubangui, 1932b
<i>Lymnaea pervia</i>	Taiwan	Tsuchimochi, 1926
<i>Lymnaea radix</i>	Taiwan	Tsuchimochi, 1926
<i>Lymnaea stagnalis</i>	Italy	Vevers, 1923
<i>Lymnaea traski</i> (?).....	California	Johnson, 1920
<i>Musculium partumeium</i>	Maryland	Krull, 1935 (e)
<i>Physa gyrina</i>	Illinois Ontario	Beaver (this paper) Fallis, 1934
<i>Physa halei</i>	Maryland	Krull, 1935 (e)
<i>Physa occidentalis</i> (?).....	California	Johnson, 1920
<i>Physa rivalis</i>	Brazil	Lutz, 1924
<i>Planorbis</i> sp.....	Brazil	Lutz, 1924
<i>Pseudosuccinea columella</i>	Illinois Maryland	Beaver (this paper) (e) Krull, 1935 (e)
<i>Viviparus</i> sp.....	Taiwan	Tsuchimochi, 1926
<i>Pisidium</i> sp.....	Illinois	Beaver (this paper) (e)
<i>Sphaerium</i> sp.....	Illinois Ontario	Beaver (this paper) (e) Fallis, 1934
<i>Stagnicola palustris</i>	Ontario	Fallis, 1934
<i>Planaria</i> sp. (?).....	California	Johnson, 1920
<i>Rana esculenta</i>	Japan	Miki, 1923
<i>Rana japonica</i>	Japan	Dollfus, 1925
<i>Rana pipiens</i> (larva).....	Illinois	Beaver (this paper)
<i>Rana pipiens</i> (adult).....	Illinois	Beaver (this paper)
<i>Rana rugosa</i>	Japan	Dollfus, 1925
<i>Rana catesbiana</i> (larva).....	Japan	Dollfus, 1925 (e)
<i>Rana nigromaculata</i>	Japan	Dollfus, 1925
"Tadpoles".....	Taiwan	Tsuchimochi, 1926
"Tadpoles" (<i>Bufo americana</i>).....	Ontario	Fallis, 1934
<i>Ameiurus melas</i>	Illinois	Beaver (this paper) (e)

TABLE 3.—*Echinostoma revolutum*, ADULT
(e = experimental infection only)

Host	Locality	Reference
<i>Anas brasiliense</i>	Brazil	Dietz, 1910
<i>Anas platyrhynchos</i> (domestic).....	Poland	Kowalewski, 1895, 1897
	Taiwan	Anazawa, 1929 (e)
	Taiwan	Iwata and Tamura, 1933
	Taiwan	Tsuchimochi, 1924
	Japan	Yamaguti, 1933
	Japan	Ishii, 1932
	Philippine Islands	Tubangui, 1932a
	England	Vevers, 1923 (e)
	England	Brown, 1926 (e)
	Turkestan	Skrjabin, 1913
	Middle-Europe	Dietz, 1910
	Illinois	Beaver (this paper) (e)
	Illinois	Miller, 1936 (e)
<i>Anas P. platyrhynchos</i> (wild).....	Japan	Ishii, 1932
	Middle-Europe	Dietz, 1910
	Illinois	Beaver (this paper)
<i>Anas superciliosa</i>	Queensland, Australia	Johnston, 1913, 1916
	Queensland	Nicoll, 1914
<i>Anser anser</i> (domestic).....	Taiwan	Iwata and Tamura, 1933
	Middle-Europe	Dietz, 1910
	Ontario	Fallis, 1934 (e)
<i>Anser cinerius</i>	Ontario	Swales, 1933a
<i>Anseranas semipalmata</i>	Queensland	Nicoll, 1914
<i>Buteo lagopus-s. johannis</i>	Illinois	Beaver (this paper)
<i>Cairina moschata</i>	Brazil	Lutz, 1924 (e)
	Brazil	Dietz, 1910
<i>Cheniscus pulchellus</i>	Queensland	Nicoll, 1914
<i>Chenopsis atrata</i>	Queensland	Nicoll, 1914
<i>Coloeus monedula</i>	Poland	Markowski, 1933
<i>Columba domestica</i>	Philippine Islands	Tubangui, 1932b (e)
	Germany	Krause, 1925a (<i>Echinostoma</i> sp.)
	Germany	Zunker, 1925 (<i>E. columbae</i>)
	Germany	Bolle, 1925 (<i>E. columbae</i>)
	Germany	Sprehn, 1927 (<i>E. paraulum</i>)
	Illinois	Beaver (this paper) (e)
<i>Colymbus cristatus</i>	Middle-Europe	Dietz, 1910 (<i>E. paraulum</i>)
<i>Coracias garrula</i>	Egypt	Looss, 1899
<i>Corvus cornix</i>	Poland	Markowski, 1933
<i>Dendrocygna viduata</i>	Brazil	Dietz, 1910 (<i>E. mendax</i>)
"Duck".....	Ontario	Swales, 1933b (corrected)
<i>Gallus gallus</i> (domestic fowl).....	Turkestan	Skrjabin, 1913
	Taiwan	Tsuchimochi, 1924
	Taiwan	Anazawa, 1929 (e)
	Japan	Ishii, 1932
	Japan	Kuriu, 1932

TABLE 3.—*Concluded*

Host	Locality	Reference
<i>Gallus gallus</i> (domestic fowl) cont'd..	Japan Poland Middle-Europe Illinois	Iwata and Tamura, 1933 Kowalewski, 1895, 1897 Dietz, 1910 Beaver (this paper) (e)
<i>Mareca americana</i>	Alberta, Canada	Beaver (this paper)*
<i>Mareca penelope</i>	Middle-Europe	Dietz, 1910
<i>Marila marila</i>	California	Johnson, 1920
<i>Meleagris gallopavo</i>	Ekaterinburg, U.S.S.R.	Skrjabin, 1915
<i>Neochen jubata</i>	Brazil	Dietz, 1910 (<i>E. mendax</i>)
<i>Nyroca fuligula</i>	Japan	Yamaguti, 1933
<i>Nyroca marila</i>	California	Johnson, 1920
<i>Oidemia nigra</i>	Middle-Europe	Dietz, 1910
<i>Pernis apivorus</i>	Egypt	Looss, 1899
<i>Philomachus pugnax</i>	Egypt	Looss, 1899
<i>Scolopax rusticola</i>	Ekaterinburg, U.S.S.R.	Skrjabin, 1915
"Swan".....	Taiwan	Iwata and Tamura, 1933
<i>Tadorna tadorna</i>	Middle-Europe	Dietz, 1910
<i>Canis familiaris</i>	Taiwan Taiwan Illinois	Tsuchimochi, 1924 (e) Anazawa, 1929 (e) Beaver (this paper) (e)
<i>Cavia porcellus</i>	Illinois Maryland	Beaver (this paper) (e) Krull, 1935 (e)
<i>Epimys norvegicus</i>	Japan Taiwan Illinois	Dollfus, 1925 (<i>E. cinetorchis</i>) Tsuchimochi, 1924 (e) Beaver (this paper) (e)
<i>Felis domestica</i>	Illinois	Beaver (this paper) (e)
<i>Homo sapiens</i>	Taiwan	Anazawa, 1929
<i>Mus musculus</i>	Taiwan Illinois	Anazawa, 1929 (e) Beaver (this paper) (e)
<i>Ondatra zibethica</i>	Pennsylvania Nebraska Ontario Quebec Alberta Pennsylvania Illinois Colorado Maryland	Leidy, 1888 Barker, 1915 (<i>E. armigerum</i> and <i>E. coalitum</i>) Law and Kennedy, 1932 (<i>E. armigerum</i> and <i>E. coalitum</i>) Beaver (this paper)* Beaver (this paper)* Beaver (this paper)† Beaver (this paper) Beaver (this paper)† Krull, 1935 (<i>E. coalitum</i>)
Rabbit (domestic).....	Illinois Maryland	Beaver (this paper) (e) Krull, 1935 (e)
<i>Sus scrofa</i>	Illinois	Beaver (this paper) (e)

*Collected by W. E. Swales.

†Records obtained from a study of specimens in the collection of Henry B. Ward.

TABLE 4.—SUMMARY OF REINFECTION EXPERIMENTS

Host	Days infected	Dates of infections	Remarks
Im 1.....	6	10/3 —10/9	5 worms administered <i>per anus</i>
	12	10/12—10/24	12 worms administered <i>per anus</i>
	?	11/2 —	Negative by fecal examinations
	?	11/22—	Negative by fecal examinations and autopsy 12/15
Im 2.....	15	10/5 —10/20	Positive by fecal examination from 10/15 to 10/20
	6	10/24—10/30	1 worm administered <i>per anus</i>
	?	11/2 —	Negative by fecal examination
	8	12/6 —12/14	1 immature worm recovered
Im 3.....	24	10/8 —11/1	10 worms administered <i>per anus</i>
	16	11/2 —11/18	Positive by fecal examination from 11/2 to 11/18
	10	11/6 —12/16	3 immature worms recovered
Im 4.....	26	10/2 —10/28	6 worms administered <i>per anus</i>
	32	11/2 —12/4	Positive by fecal examination from 11/18 to 12/5
	?	12/6 —	Negative by autopsy on 12/15
Im 5.....	28	10/24—11/22	1 worm administered <i>per anus</i>
	18	12/10—12/28	2 mature worms recovered
Im 6.....	40	10/18—11/28	1 worm administered <i>per anus</i>
	21	12/10—12/31	11 mature worms recovered
Im 7.....	20	10/24—11/14	1 worm administered <i>per anus</i>
	?	12/10—	Negative by fecal examination and autopsy on 12/27
Im 8.....	?	10/24—	1 worm administered <i>per anus</i> ; probably expelled immediately
	19	12/10—12/29	1 worm recovered, mature

TABLE 5.—EXPERIMENTS IN WHICH CERCARIAE OF COMMON PARENTAGE WERE FED TO BIRDS AND MAMMALS

Exp. no.	Cercaria used	Host	Number of worms	Age in days	Position in host
1	C3-A	Pigeon 7	621	11	Anus to proventriculus
		Rabbit 2	284	4	Cecum to duodenum
2	C4-28	Pigeon 10	18	13	Middle ileum
		Rabbit 4	122	7	Lower and middle ileum
3	C4-16	Rabbit 5	28	17	Lower and middle ileum
		Rabbit 6	0	0	
		Pigeon 11	0	?	?
4	C5-A	Rabbit 3	540	8	Cecum to duodenum
		Pigeon 9	580	11	Anus to duodenum
		Dog 1	7	18	Cecum and lower ileum
5	C6-2	Chicken 5	46	13	Middle and lower ileum
		Dog 3	64	23	Lower part of middle ileum
		Cat 5	3	2	Lower ileum
		Rat 30	0	0	
		Rat 31	0	0	
6	C6-3	Chicken 6	2	16	Cloaca
		Cat 2	39	13	Lower ileum
		Pigeon 19	93	21	Middle and upper ileum
7	C6-5	Rabbit 8	5	17	Middle ileum
		Pigeon 16	291	15	Middle and upper ileum
		Mice 14-17	0	0	
8	C6-6	Chicken 7	1	11	Lower ileum
		Guinea pig 1	354	11	Upper colon to stomach
		Rat 25	0	0	
		Rat 26	30	12	Middle ileum
9	C6-7	Rabbit 7	29	18	Middle ileum
		Chicken 3	22	13	Cloaca, lower and middle ileum
		Pigeon 17	2	13	Middle ileum
10	C6-8	Duck 3	0	0	
		Cat 4	352	21	Lower and middle ileum
		Pigeon 18	195	14	Cloaca, rectum, and lower ileum
11	C6-9	Pigeon 15	63	14	Lower, middle, and upper ileum
		Rat 27	431	14	Lower, middle, and upper ileum
12	C6-11	Hog 2	32	12	Lower ileum
		Pigeon 13	31	15	Lower, middle, and upper ileum
		Rat 26	3?	39?	Middle ileum
13	C6-12	Hog 3	8	32	Lower ileum
		Pigeon 14	0	14-15	Host not killed
14	C6-17	Rat 28	95	15	Middle and upper ileum
		Chicken 4	30	15	Cloaca, lower and middle ileum

TABLE 6.—SUMMARY OF DATA ON HOSTS USED IN ALL EXPERIMENTS

Host no.	Cercaria used	Number of worms	Mature in days	Age of worms in days	Host type
<i>Pigeons</i>					
1	C1-A	38	..	4 and 1	
2	C1-A	300	11	11	
3	C1-A	0	11	Worms expelled on 12th day	
4	C1-A	6	10	16	
5	C3-A	0	..	Cysts not swallowed	
6	C3-B	14	..	6	
7	C3-A	621	11	11	
8	C4-mix	82	9	11	
9	C5-A	580	9	11	
10	C4-28	18	9	13	
11	C4-16	0	12	Worms expelled on 17th day	
12	C6-10	96	10	13	
13	C6-11	31	11	15	
14	C6-12	0	10	Worms expelled on 15th day	
15	C6-9	63	10	14	
16	C6-5	291	12	15 (Many immature)	
17	C6-7	2	11	13	
18	C6-8	195	11	14	
19	C6-3	93	11	21	
20	C7-4	1	..	8 (Used as T6 and Im 2)	
21	C7-4	0	..	0 (Used as T1 and Im 4)	
22	C7-4	0	..	0 (Used as T2, T4, Im 1)	
23	C7-4	3	..	10 (Used as T3 and Im 3)	
24	C6-6	0	..	0 (Used as T7 and Im 7)	
25	C6-6	2	17	18 (Used as T10 and Im 5)	
26	C6-2	1	19	19 (Used as T9 and Im 8)	
27	C6-6	11	12	21 (Used as T5 and Im 6)	
<i>Domestic Fowl</i>					
1	C4-mix	2	..	9 (Immature)	
2	C4-mix	11	14	17	
3	C6-7	22	12	13	

TABLE 6.—Continued

Host no.	Cercaria used	Number of worms	Mature in days	Age of worms in days	Host type
<i>Domestic Finch (Concluded)</i>					
4	C6-17	30	12	15	
5	C6-2	46	12	13	
6	C6-3	2	12	16	
7	C6-6	1	..	11 (Immature)	
8	C6-13	9	12	13	
<i>Domestic Duck</i>					
1	C4-10	1	..	14	
2	C4-mix	2	..	10 (Mature)	
3	C0-0	27	..	14	
4	C6-8	0 (Worms expelled)	
5	C7-3	6	9	17	
<i>Rats</i>					
1	C0-0	3-400	4	4	Wild
2	C0-0	3-400	..	1	Wild
3	C0-0	20	17	20	Wild
5	C0-0	0	18	Worms expelled on 24th day	Brown
6	C0-0	0	18	Out on 22nd day	Wild
7	C1-A	0	Neg.	..	Hooded
8	C1-A	0	Neg.	..	Albino
9	C1-A	0	Neg.	..	Albino
10	C1-A	0	Neg.	..	Wild
11	C3-B	0	Neg.	..	Hooded
12	C3-A	0	Neg.	..	Albino
13	C3-B	0	Neg.	..	Albino
14	C3-B	0	Neg.	..	Hooded
15	C3-B	0	Neg.	..	Albino
16	C4-mixed	0	Neg.	..	Hairless
17	C4-mixed	0	Neg.	(Not well fed)	Hairless
18	C4-mixed	75	19	22	Hairless

Note: Rat 4 escaped; no data.

TABLE 6.—Continued

Host no.	Cercaria used	Number of worms	Mature in days	Age of worms in days	Host type
<i>Rats</i> (Concluded)					
19	C4-mixed	124	..	16	Hairless
20	C4-6	0	Neg.	..	Hooded
21	C4-mixed	0	Neg.	..	Albino
22	C5-A	0	Neg.	..	Albino
23	C4-28	0	Neg.	..	Albino
24	C4-40	0	Neg.	..	Wild
25	C6-10	0	Neg.	..	Wild
26	C6-6	33	..	12	Wild
27	C6-9	431	..	14	Hairless
28	C6-17	95	..	15	Hairless
29	C6-13	0	Neg.	..	Wild
30	C6-2	0	Neg.	..	Wild
31	C6-2	0	Neg.	..	Wild
32	C7-4	0	Neg.	..	Yellow
33	C7-4	0	Neg.	..	Blue
34	C7-4	0	Neg.	..	Hooded
<i>Mice</i>					
1	C0-0	350	..	2	Black
2	C0-0	2	..	3	Albino
3	C0-0	0	Neg.	..	Yellow
4	C0-0	500	..	9 (None mature)	Yellow
5	C1-A	0	Neg.	..	Black
6	C0-0	0	Neg.	..	Yellow
7	C0-0	0	Neg.	..	Yellow
8	C1-A	0	Neg.	..	Yellow
9	C4-mixed	10	..	7	Yellow
10	C4-40	1	..	12 (Immature)	Wild
11	C4-40	0	Neg.	..	Wild
12	C6-5	0	Neg.	..	Wild
13	C6-5	0	Neg.	..	Wild
14	C6-5	0	Neg.	..	Wild
15	C6-5	0	Neg.	..	Wild

TABLE 6.—*Concluded*

Host no.	Cercaria used	Number of worms	Mature in days	Age of worms in days	Host type
<i>Rabbits</i>					
1	C5-A	75	..	1	Albino
2	C3-A	284	..	4	Albino
3	C5-A	540	..	8	Albino
4	C4-28	122	..	7	Albino
5	C4-16	28	12	17	Wild
6	C4-16	0	..	(Not well fed)	Chocolate
7	C6-7	29	12	18	Wild
8	C6-5	5	12	17	Wild
<i>Dogs</i>					
1	C5-A	7	..	18 (Immature)	Collie
2	C4-mixed	700	..	8	Setter
3	C6-2	64	22	23	Setter
<i>Cats</i>					
1	C4-40	0	16?	(Expelled on 17th day)	Mongrel
2	C6-3	39	..	13	Mongrel
3	C6-13	1	..	2	Black
4	C6-8	352	18	21	Mongrel
5	C6-2	3	..	2	Mongrel
6	C6-6	0	?	(None present on 26th day)	Mongrel
<i>Hogs</i>					
1	C6-10	1	..	12	Hampshire
2	C6-11	32	..	12	Hampshire
3	C6-12	8	..	32	White
4	C6-8	(Gut mixed by butcher)	White
<i>Guinea pigs</i>					
1	C6-6	354	(Few with ova in the uterus when autopsied on the 11th day)		

TABLE 7.—RATE OF DEVELOPMENT IN THE EXPERIMENTAL HOSTS

Host	Body temperature (Approximate)	Days required to reach maturity	
		Range	Average
Rat.....	100	17-19	18
Mouse ¹
Rabbit.....	102	12	12
Dog.....	101.5	22	22
Cat.....	102	16 ² -18	18
Hog.....	102	32	32
Guinea Pig.....	101.7	11	11 ³
Duck.....	110	10-11	10.2
Fowl.....	107-109	12-14	12.5
Pigeon.....	106-108	9-12 ³	11
All mammals.....	11-32	19
All birds.....	9-14	11

¹No mature worms taken.²Worms almost mature, eggs in uterus but none in host's feces.³Pigeons with reinfection required longer than 12 days.TABLE 8.—COLLECTIONS OF *Helisoma trivolvis* IN THE VICINITY OF URBANA, ILLINOIS

Collection number	Date	Source	Number collected	Number infected
C1.....	6/ 9/33	Camp Creek, Seymour	14	1
C2.....	6/20/33	Drainage ditch at Crystal Lake Park	35	0
C3.....	7/ 8/33	First north tributary of Salt Fork, West of Homer Park	14	2
C4.....	8/ 1/33	Camp Creek, Seymour	100	43
C5.....	8/ 5/33	Leverette, Illinois, Drainage Ditch	41	1
C6.....	9/11/33	Camp Creek	72	38
C7.....	10/28/33	Camp Creek	9	1
C8.....	3/10/34	Camp Creek	12	1

TABLE 9.—TRANSFER EXPERIMENTS

Transferred from	Transferred to	Number of worms	Days in original	Days in second	Total age in days
Chicken 5.....	Pigeon T1	6	13	26	39
Rabbit 7.....	Pigeon T2	5	18	6	24
Dog 3.....	Pigeon T3	10	23	24	47
Pigeon 18.....	Pigeon T4 (T2)	10	14	12	26
Pigeon 19.....	Pigeon T5	1	21	40	61
Rat 26.....	Pigeon T6 (14)	1	39	6	45
Rat 26.....	Pigeon T7	1	12	20	32
Rat 26.....	Pigeon T8	1	12	23	35
Rat 26.....	Pigeon T9	1	12	?	?
Rat 26.....	Pigeon T10	1	12	28	40

EXPLANATION OF CHARTS

The charts serve three separate purposes. Charts 1, 2, 3, 4, 5, 6, 7, 19, and 20 give the average measurements for specimens of any given size under 20 mm. The range of variability that is due to factors other than host is best shown on Charts 8, 9, 10, 11, 12, 13, 14, 19, and 20, where measurements of individual worms are plotted separately. Charts 7, 8, 9 and 10, 11 and 12, 13 and 14, 15, 16, 17, 18, 19 and 20, and especially 8, serve to show the differences and similarities to be found in specimens taken from the two types of hosts in which they commonly occur in the adult stage.

The curves are made from lines drawn through points obtained by averaging all of the individual points within arbitrary limits. The lines radiating from zero are drawn through points of equal proportion and this proportion is indicated in each case on the line as 1:2, 1:3, etc.

Chart 1 shows the diameter of the acetabulum and the width of the body in relation to the total length of the body. The former shifts from one-fifth in very small worms to about one-sixteenth the body length in specimens over 13 mm in length. Similarly the body width shifts from one-third to nearly one-tenth.

Chart 2 shows the size relationship between the acetabulum and the collar. The acetabulum is the larger in worms over 4 mm in length.

Chart 3 shows the size relationship between the acetabulum, oral sucker, and collar. The body length may be determined from Chart 1, and the relative size of the pharynx may be seen in Charts 19 and 20.

Chart 4 shows the relative lengths of the three regions of the body limited by the acetabulum and the ovary.

Chart 5 shows the relative size of the gonads in relation to the body length.

Chart 6 shows the relative length of the lateral posterior ventral collar spine (see Text-figs. 3 and 5) in relation to the body length.

Chart 7 shows the relationship between the body length and the length of the cuticular spines in specimens from the two types of hosts.

Chart 8 shows the relationship between the body length and the number of complete rows of dorsal cuticular spines (see Text-fig. 2) in specimens from the two types of hosts. In this chart the lengths of the individuals having the same number of complete rows have been averaged and the total number within the class indicated by a number near each point.

Charts 9 and 10 show the relationship between the body length and the greatest width of the body in specimens from the two types of hosts. The larger worms are slightly stouter in bird hosts.

Charts 11 and 12 show the size relationship between the body length and the acetabulum in specimens from the two types of hosts. The acetabulum is slightly smaller in the smaller specimens from mammals.

Charts 13 and 14 show the length relationship between the whole body and the pre-acetabular region in specimens from the two types of hosts. Differences here appear to be insignificant.

Chart 15 shows the length relationship between the body and the region of the uterus. It appears here that there is no significant difference in the length of this region in the specimens from the two types of hosts.

Chart 16 shows the length relationship between the body and the post-ovarian region in specimens from the two types of hosts. The greater length of this region in larger specimens from bird hosts is probably significant.

Chart 17 shows the difference in the size relationship between the acetabulum and the collar in specimens from the two types of hosts.

Chart 18 shows the size relationship between the acetabulum and the oral sucker in specimens from the two types of hosts. The oral sucker is relatively larger in the larger specimens from birds.

Charts 19 and 20 show the size relationship between the pharynx and the oral sucker. The variation in this character in the specimens from the two types of hosts is probably not significant.

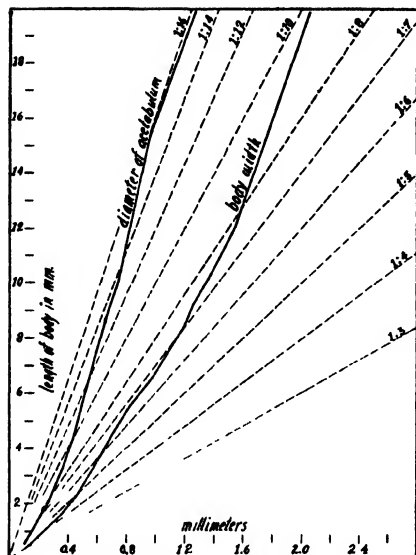


CHART 1

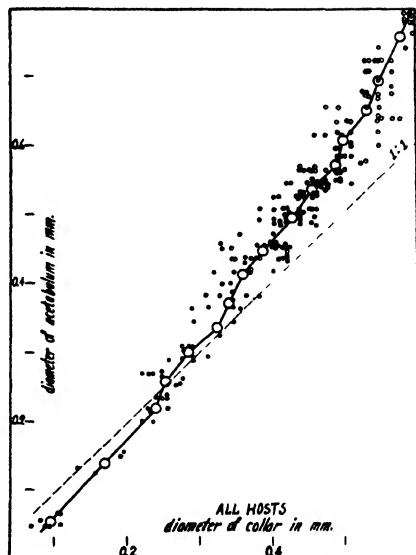


CHART 2

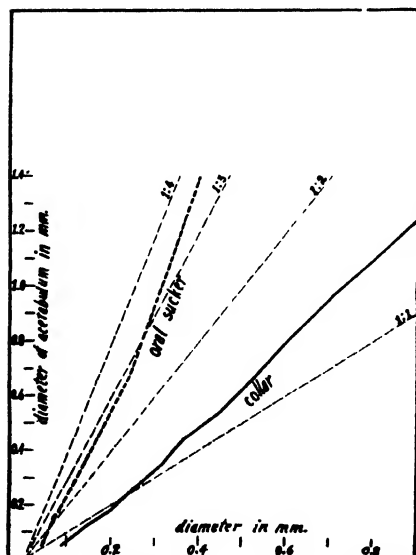


CHART 3

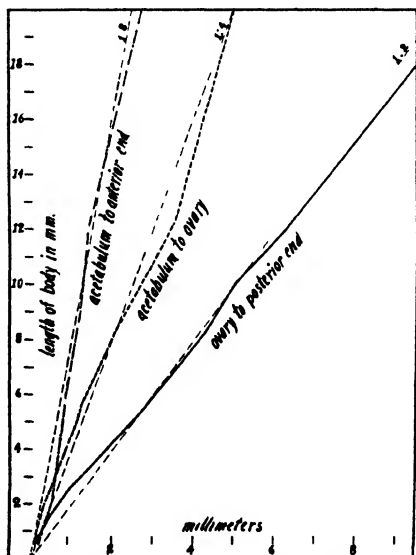


CHART 4

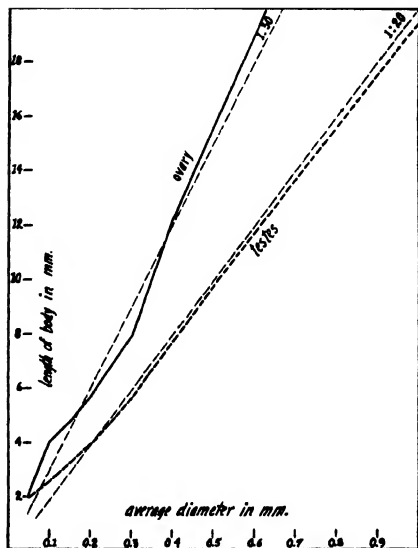


CHART 5

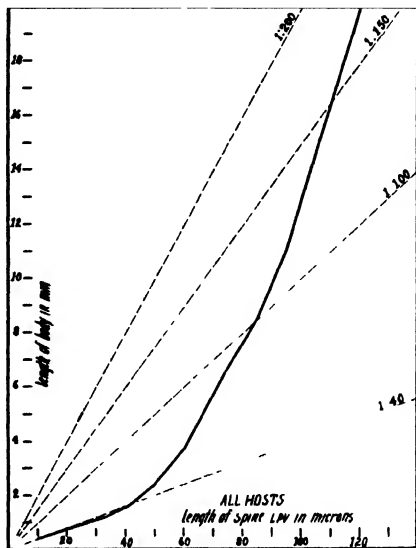


CHART 6

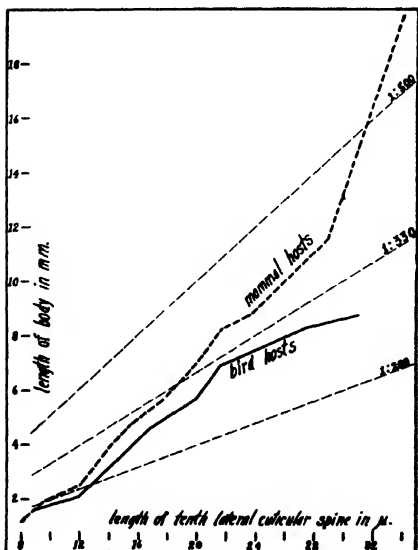


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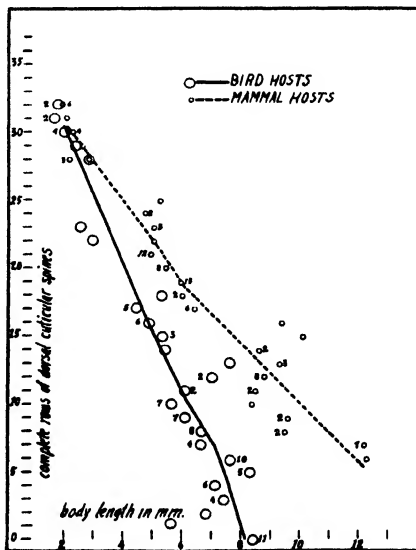


CHART 8

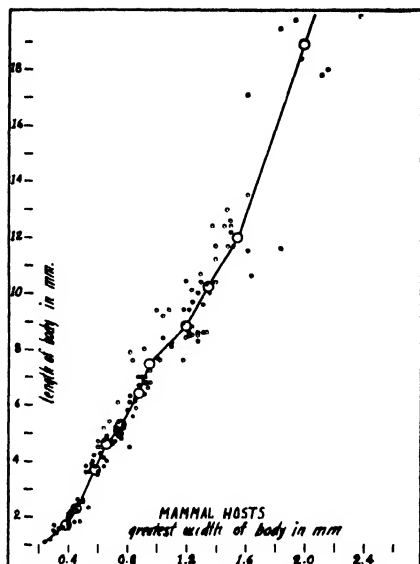


CHART 9

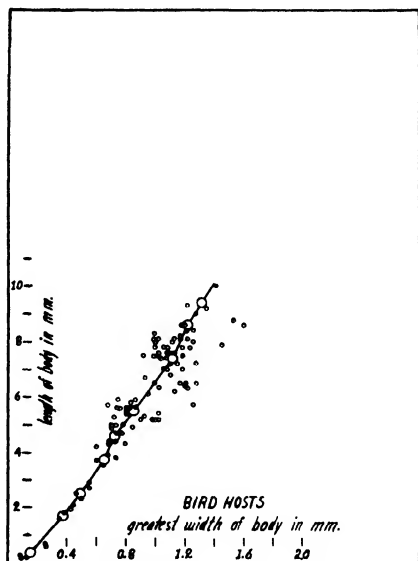


CHART 10

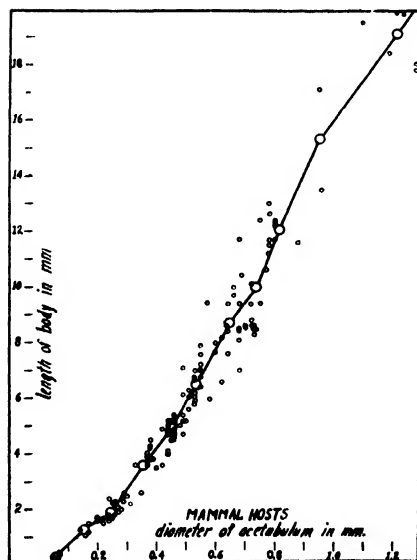


CHART 11

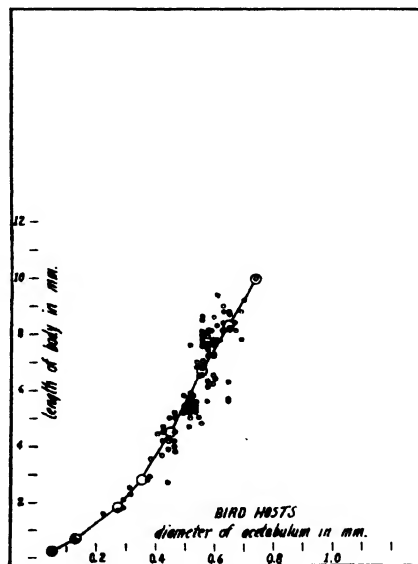


CHART 12

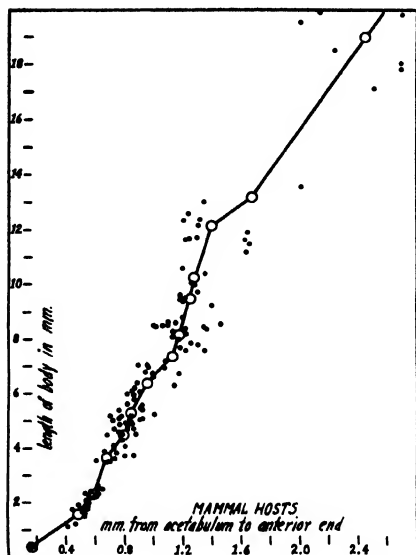


CHART 13

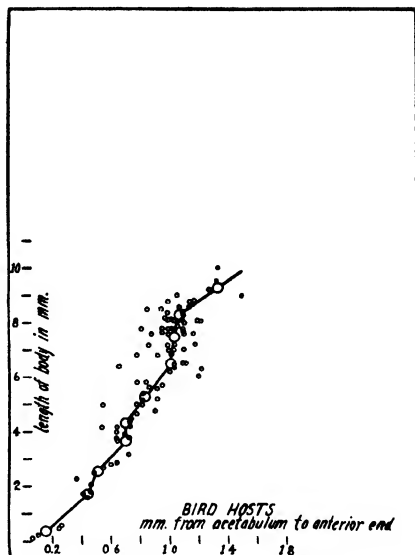


CHART 14

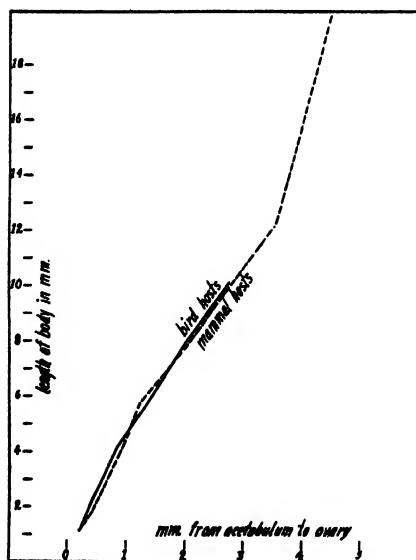


CHART 15

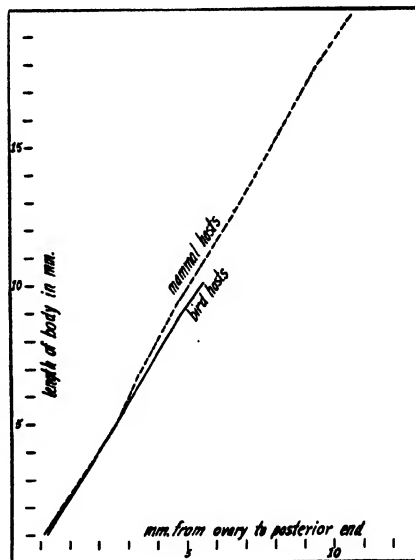


CHART 16

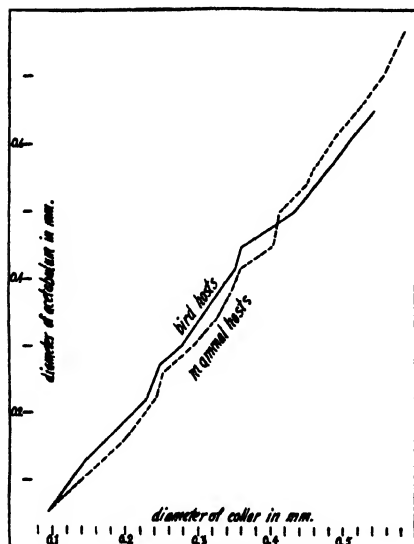


CHART 17

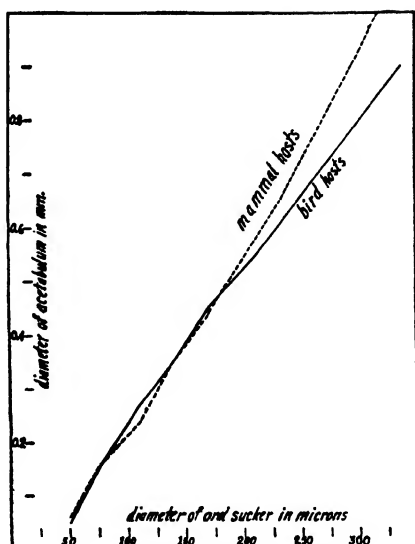


CHART 18

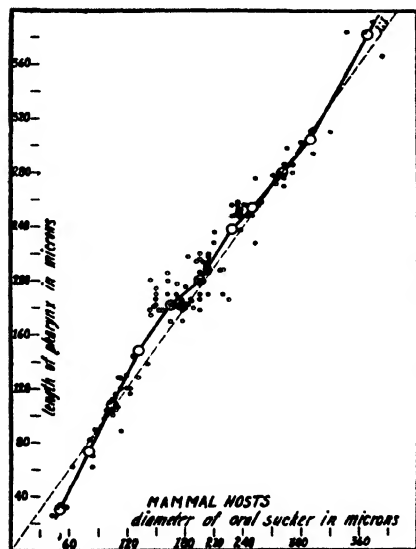


CHART 19

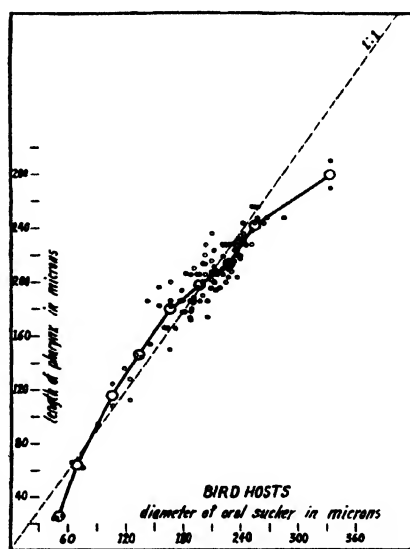


CHART 20

PLATE 1

FIGS. 1, 2, 3.—Head of cercaria, showing cephalic spination in lateral, ventral, and dorsal views, respectively. (Camera lucida drawings).

FIG. 4.—Camera lucida drawing of a fixed specimen of the cercaria.

FIG. 5.—Diagram of tadpole showing the usual course followed by creeping cercariae.

FIG. 6.—Diagram showing the cephalic ducts as seen in the unflattened specimen (cercaria).

FIG. 7.—Diagram of the cuticular plates of the miracidium in dorsal view.

FIG. 8.—Camera lucida drawing of the partially contracted tail of the cercaria. Lateral view.

FIG. 9.—Camera lucida drawing of the head of an 8.55 mm adult from a chicken.

FIG. 10.—Camera lucida drawing of the tip of the tail of a fixed cercaria, showing the extent of the circular muscles and the fin fold membrane.

FIG. 11.—The miracidium, almost mature within the egg. Outlines made with the camera lucida, details free-hand.

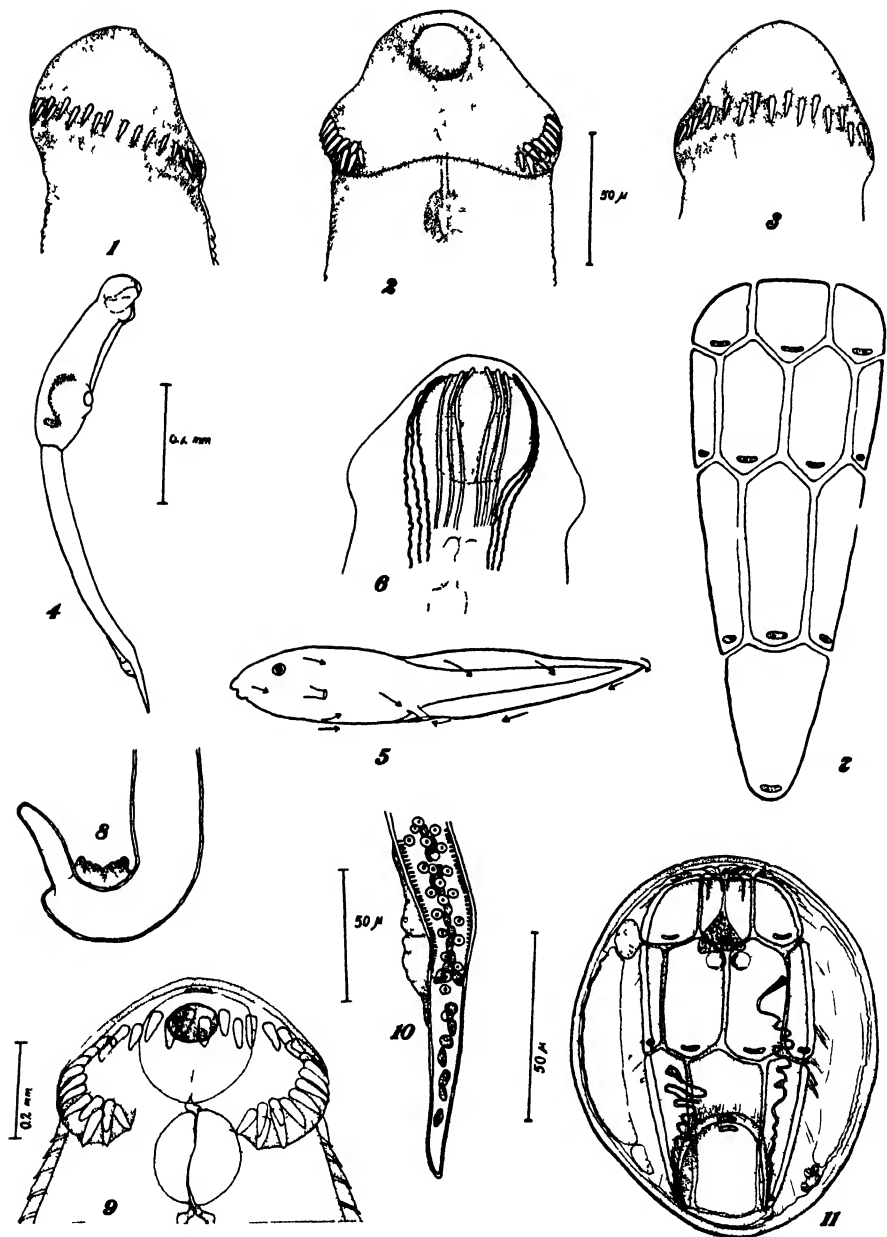


PLATE I

PLATE II

FIG. 12.—Camera lucida drawing of a fixed specimen of the cercaria, ventral view. Excretory system added free-hand from drawings made from living specimens.

FIG. 13.—Camera lucida drawing of a 20 mm specimen from a muskrat. Ventral view.

FIG. 14.—Camera lucida drawing of an 8.8 mm specimen from a chicken, experimentally infected. Ventral view.

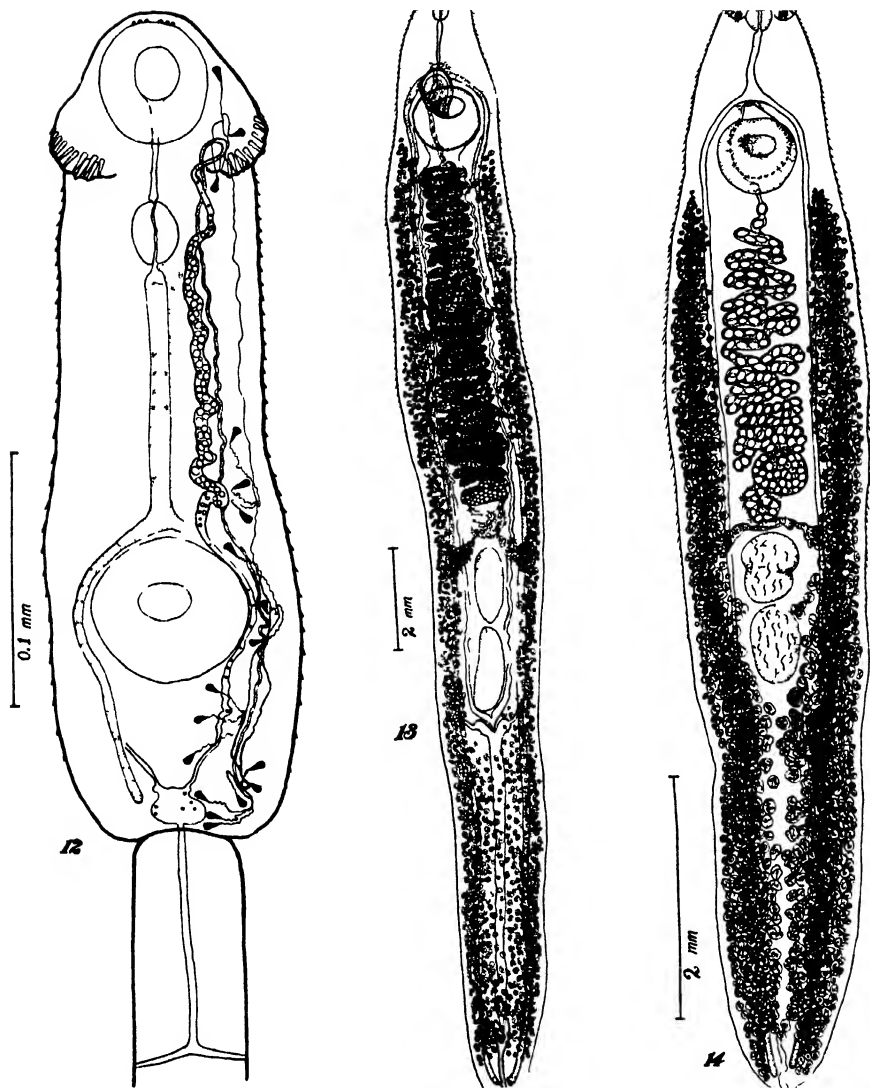


PLATE II

PLATE III

FIG. 15.—Cephalic spines of *Echinostoma cinetorchis*. Text-fig. 1, Ando and Ozaki, 1923. (From Dollfus, 1925, text-fig. 2.)

FIG. 16.—Cephalic spines of *E. mendax*. (From Dietz, 1910, text-fig. A.)

FIG. 17.—Cephalic spines of *E. paraulum*. (From Dietz, 1910, text-fig. B.)

FIG. 18.—Cephalic spines of *E. echinocephalum*. (From Dietz, 1910, text-fig. C.)

FIG. 19.—Cephalic spines of *E. columbae*. (From Bolle, 1925, text-fig. 1.)

FIG. 20.—Cephalic spines of *E. columbae*. (From Zunker, 1925, text-fig. 2. Scale is 0.1 mm.)

FIG. 21.—Cephalic spines of *Echinoparyphium* (?*Echinostoma*) *paraulum*. (From Sprehn, 1932, text-fig. 8.)

FIG. 22.—*Echinostoma miyagawai*. (From Ishii, 1932, Plate II, fig. 10.)

FIG. 23.—Cephalic spines of *E. miyagawai*. (From Ishii, 1932, Pl. II, fig. 11.)

FIG. 24.—*Echinostoma columbae*. (From Zunker, 1925, text-fig. 1. Scale is about 1 mm.)

FIG. 25.—Cephalic spines of *E. echinatum* (= *revolutum*). (From Kowalewski, 1895, Plate 8, fig. 1.)

FIG. 26.—"*Fasciola revoluta*" (= *Echinostoma revolutum*) as figured in the original description. (From Froelich, 1802, Plate II, fig. 7.)

FIG. 27.—Cephalic spines of *E. sudanense*. (From Odhner, 1911, Plate III, fig. 13.)

FIG. 28.—Cephalic spines of *E. echinatum* (= *revolutum*) from a goose. (From Looss, 1899, Plate XXIV, fig. 7.)

FIG. 29.—Cephalic spines of *E. echinatum* (?syn. *limicoli*) from *Machetes pugnax*. (From Looss, 1899, Plate XXIV, fig. 6.)

STUDIES ON ECHINOSTOMA—BEAVER

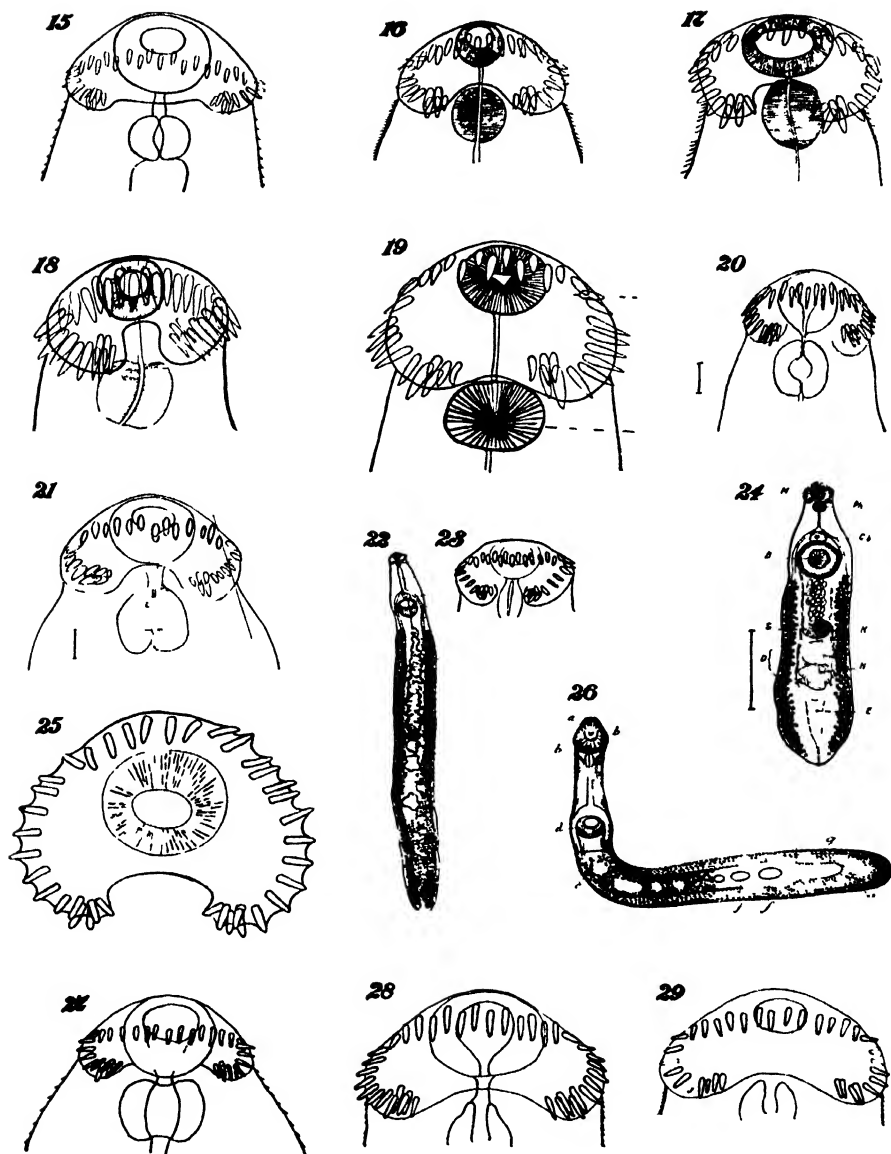


PLATE III

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**A GENERIC CLASSIFICATION
OF THE NEARCTIC SAWFLIES
(HYMENOPTERA, SYMPHYTA)**

WITH SEVENTEEN PLATES

BY

HERBERT H. ROSS

**Contribution No. 188 from the Entomological Laboratories of the
University of Illinois, in Cooperation with the
Illinois State Natural History Survey**

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INTRODUCTION

Few problems in the Hymenoptera have been so disputed as the general classification of the sawfly groups. Practically no two authors have agreed either on the subject of major groupings or the basic reasons for their divisions. The present study is an attempt to find fundamental morphological evidence which will separate the sawflies into groups and show the paths of evolution followed in their development. While such a study is almost necessarily incomplete without a lifetime of work, nevertheless structures have been found which show definitely some of the relationships and groupings of these insects. It is, I believe, the first time such a study has been based on the comparative morphology of the body and its appendages, rather than on only those characters which may be seen without dissection. It seems worth while to present these findings now in an endeavor to put the classification of the sawflies on a more stable basis.

Another grave difficulty confronting the North American sawfly worker has been the almost total lack of illustrated keys to the genera. Little effort has been made in the past to correlate the generic names used in various parts of the world, so that in many cases a considerable re-shuffling has been imperative. The solution of these problems has been linked very closely with the classification of the higher categories.

In the unravelling of these problems, palæontology has given us no clues, since the earliest known hymenopterous fossils belong to specialized groups which occur at the present day. These include such families as the Cephidae, Orussidae, and Siricidae. Fossils showing the nature of the earliest and most primitive Hymenoptera are still unknown. The utilization of embryological evidence has been impossible because of lack of material except in very few instances; and it is doubtful if a great deal could be learned from this source. This has left open only one avenue of approach, comparative morphology. The problem has therefore resolved itself into piecing together evidence drawn only from the differences and similarities found in the parts of those sawflies existing at the present day.

METHODS

A large number of the drawings were made from pinned specimens. This is especially true of the characters used in generic keys, such as antennae, tarsi, sheaths, etc. The remainder were made from cleared specimens. The specimens were soaked in 25 per cent caustic potash (KOH) for three to twenty-four hours, depending on their darkness, hardness, etc. The male genitalia were preserved in glycerine in small vials; the saws, wings, and legs were mounted in either balsam or euparal on slides; and the larger structures were preserved in 80 per cent ethyl alcohol.

MATERIALS

The taxonomic portion of this study is based on an examination of about 50,000 sawflies, including 90 per cent of the types of nearctic species. This material has been accumulated through the courtesy of the officers of the following institutions: Academy of Natural Sciences of Philadelphia; Brigham Young University; California Academy of Sciences; Canadian National Museum; Colorado Agricultural College; Cornell University; Deutsches Entomologische Institut; Entomological Branch, Canadian Department of Agriculture; Field Museum of Chicago; Illinois State Natural History Survey; Iowa State College; Iowa Wesleyan College; Kansas State Agricultural College; MacDonald College; McGill University; Montana State Agricultural College; New York State Museum; Ohio State University; Oregon Agricultural College; Purdue University; South Dakota Agricultural College; Texas Agricultural College; United States National Museum; University of Alberta; University of British Columbia; University of Colorado; University of Idaho; University of Illinois; University of Kansas; University of Michigan; University of Nebraska; University of Oklahoma; University of Wisconsin; Washington Agricultural College.

MORPHOLOGY

The first work to be published dealing with the comparative morphology of sawflies was Hartig's "Die Familien der Blattwespen und Holzwespen" in 1837. This contains descriptions and many illustrations of the mouthparts, antennae, and other miscellaneous characters. It is, in fact, a veritable classic of sawfly morphology.

Since that time several workers have greatly increased our knowledge of sawfly morphology. Cameron in various papers (1882, etc.) gave descriptions and illustrations of many parts in other species. Van Dine (1906) described and illustrated the mouthparts of *Pamphilius*; MacGillivray (1906) made an exhaustive study of the wings of sawflies; Snodgrass (1911) illustrated the thoracic structure of many forms; Crampton (1919) described and illustrated almost all types of male genitalia found in the group; Boulonge (1924) made a remarkably fine study of the male genitalia, with special reference to the muscles and their attachment; Bird (1926) made a detailed morphological study of *Hoplocampa halcyon* (Norton); and Taylor (1931) has made a complete histological and internal anatomical study of the head of a few species of Tenthredinidae. Marlatt (1896), Smulyan (1923), Middleton and Rohwer (in several papers) have made some morphological studies, mostly in connection with taxonomic work. Aside from these, references to sawfly morphology are scattered in general texts and papers on insect anatomy and phylogeny.

In the following discussion no attempt is made to offer a complete treatise on sawfly morphology. Only those characters have been discussed which, on close study, appeared to offer differences indicating relationships of groups, or to possess differences which might be used in such a capacity at a later date. The following parts have been studied and illustrated in greatest detail: the head, its endoskeleton and appendages; the external anatomy of the thorax and first two abdominal segments; the wing venation and the male genitalia. In addition to these major parts some other characters, such as tibial spurs, have been of considerable help in corroborating the phylogenetic arrangements presented herein.

HEAD AND APPENDAGES

Head Capsule

The head is always hypognathous, having the mouthparts directed downwards in repose. They may be directed forward when in use, but this is caused by a swinging forward of the entire head in a pendulum motion, the hinge being partly at the odontoidea and partly at the dorsal margin. This latter point of articulation is due to the moving of the head and "atlas" together (see p. 23).

Many sutures and sclerites found in the heads of primitive insects are obsolescent or entirely absent in the heads of sawflies. See Plate I, figs. 1, 2. Not only this, but no other parts have been added. The epicranial suture (ep) is present in only a few forms (e.g., Pergidae, Megalodontidae), and in these it is only a crease ending at a point between the lateral ocelli. The clypealiae and mandibulariae are entirely absent. The clypeus (cl) is not divided transversely into a pre- and postclypeus. It is separated from the front (f) by a furrow instead of a well-marked suture, and separated from the genae (g) by a suture or furrow. The lateral arms of the epicranial sutures are lacking, so that the definition of the vertex and front is practically impossible. The anterior aspect of the head, however, is provided with several furrows, ridges, and areas which bear a fixed relation to the ocelli, eyes, base of antennae, and tentorinae. These have been given a terminology by Marlatt, Rohwer, and MacGillivray; and although the names bear no relation to the hypothetical areas of the head, they are of great use in taxonomic description.

The antennal sclerites are usually fused with the surrounding head capsule, but sometimes separated from it by a suture which is more or less visible when the head is cleared in potash. The antennae, fig. 1, articulate with a distinct antacola, which is peg-shaped and located on the ventral or meso-ventral margin of the antennal socket. The oculata or eye sclerite, fig. 17 (oc), is not visible externally, but consists of an internal, converging, sclerotized shelf upon which the eye rests. The compound eyes (e) themselves are always large, composed of a very large number of facets. Three ocelli (o) are always present, situated between the dorsal portions of the compound eyes.

In the Siricoidea, Plate II, fig. 18, a groove (gr) is present, running ventrad or caudad of the antennal sockets, which receives the basal segments of the antennae in repose.

On the posterior margin of the head of all sawflies the occipital and occipitopostgenal sutures are both absent. A distinct crassa (cr) is frequently present, originating at the postcoila of the mandible (ptc), extending dorsad and sometimes completely encircling the occipital region, fig. 2. It is always represented by a rounded, elevated portion if it is not present as a distinct ridge. The maxillariae (mx) are always present, defined by distinct furrows or sutures, and each is provided with an odontoidea (od), which articulates with the cervicum. The ventral end of the maxillariae bears the paracola, upon which the maxillae articulate. In those forms possessing a genapont the maxillariae are confined to the margins of the occipital foramen and the paracoliae are not in evidence, fig. 19.

Sawfly heads vary considerably in shape, size, and sturdiness, in the relative positions of eyes and antennae, width of malar space, and many other points. These, however, are more useful in a study of taxonomy

than in morphology and will not be discussed further here. The most important matter is a consideration of the structure and origin of the types of head, which have a significant bearing on the relationships of the various groups of sawflies.

HEAD TYPES.—Four types of head are found, figs. 2, 5, 8, 19, characterized by the manner in which the genae or other parts are formed around the oral cavity or maxacava, and the occipital foramen. These types are termed *open*, fig. 2, *maxapontal*, fig. 8, *genapontal*, fig. 19, and *closed*, fig. 5, on a descriptive basis.

Open Head, figs. 1 and 2.—This is the simplest type, from which all the other types are derived. Maxillariae long and slender, not united on the meson, the dorsal half bearing the odontoidea, the ventral margin bearing a small process, the paracoila. Postgenae neither produced mesally, nor over-lapping the maxillariae. This results in the occipital foramen being continuous with the maxacava, or oral cavity. The sides and anterior margin of the clypeus are free and the mandibles are never encircled at the base by the head capsule. This type occurs in the superfamily Tenthredinoidea and the families Xyelidae and Blasticotomidae. In the Tenthredinoid family Cimbicidae the maxillariae are very large, but are not fused together on the meson as they appear to be at first glance.

Maxapontal Head, figs. 7, 8.—Similar to the above type but with the ventral portion of the maxillariae fused on the meson, forming a bridge (maxaponta, mp) between the postgenae. The maxacava is therefore separated from the occipital foramen. This type is found in the family Cephidae.

Most of the Ichneumonoidea, figs. 10, 11, have a head similar in type to the Cephoid head, differing in having the fused maxillariae and the mesal margins of the postgenae produced at an angle into the interior of the head, forming a wide shelf upon which the maxillae and labium are folded in repose. The basin-like area thus formed has been called the "trophacava" by Salman (1929). It seems to me that this term is unnecessary and that MacGillivray's prior term "maxacava" can be applied equally well, irrespective of the type of head, to that region between the postgenae into which the maxillae and labium are folded in repose. The fusion of postgenae or maxillariae on the mesal line serves only to restrict this area without altering its position or function. If the different conditions of the maxacavae are to be named, it would seem better to apply adjectives to the name maxacava as they have been applied to antennae of different shapes.

Closed Head, figs. 4, 5.—This is a most curious head capsule. The ventral portion of the maxillariae (mx) are joined on the meson, forming a broad bridge between the postgenae, and separating the occipital for-

amen from the maxacava. The postgenae are produced meso-ventrally, the entire clypeus is folded back under the ventral side of the head, and the lateral areas of the clypeus are fused with the triangular, meso-ventral areas of the postgenae. The head, therefore, instead of being open on the ventral side, has only three small openings in its wall of armour through which the mouthparts protrude—two small, lateral holes through which the mandibles protrude, and a larger circular, median one which represents the maxacava and receives the maxillae and labium. The labrum is attached to the ventral margin of the maxacava (which is also the distal margin of the clypeus) and is directed posteriorly, covering the apex of the labium in repose. This type of head is restricted in the sawfly groups to the families Megalodontidae and Pamphiliidae. It must have evolved from the open type, but no intermediate steps have been observed.

Genapontal Head, figs. 18, 19.—The diagnostic character of the heads placed in this category is the presence of a true genaponta (gp). The postgenae have been produced mesad and have united on the meson, divided only by a postgenal suture, and form a bridge across the back of the head. This separates the occipital foramen from the maxacava. The maxillariae (mx) have apparently been squeezed dorsad and lie around the ventral and lateral margins of the occipital foramen. The odontoidea (od), as usual, are borne by them. This type of head is characteristic of the superfamily Siricoidea, including the family Orussidae. In *Syntexis*, fig. 20, and *Xiphydria* the genaponta is very narrow, representing an intermediate in its formation.

The heads of the Siricoidea present a very fine example of the migration of parts, culminating in the condition found in the Orussidae. The Orussid head has been considered by most authors as representing a type very distinct from all other sawfly heads, but a critical analysis shows it to be the final product in a rather well marked chain of modifications. These are concerned with the cephalic aspect of the head which develops (1) a distinct groove for the reception of the basal segments of the antennae in repose, fig. 18, gr, and (2) the migration of the clypeus, antennal sockets, and part of the frontal region to the ventral aspect of the head.

In *Syntexis* and *Xiphydria*, figs. 20, 21, 22, the more primitive genera in the superfamily, the antennae are inserted midway between the supratentorina and the pretentorina, and well up on the cephalic aspect; the antennal groove is very shallow, extending ventro-laterad of the antennal sockets, and not definitely marked at its lower extremity on the ventral margin of the head; and the clypeus is only slightly turned underneath. In the Siricidae, fig. 18, conditions are much different. The antennal sockets have migrated ventrad, and are adjacent to the pretentorina and distant from the supratentorina; the antennal grooves are much deeper

and well marked for their entire length; and almost half of the clypeus has turned under itself, so that it forms a shelf which almost completely hides the labrum. In *Orussus*, figs. 23, 24, this migration has gone much farther. The entire clypeus and the portion of the front bearing the antennae have become turned under and now form part of the ventral aspect of the head; the antennal grooves extend along the ventral aspect and some distance up the caudal aspect; but the eyes and ocelli have assumed a more dorsal position than in either the Xiphydriidae or Siricidae.

Tentorium

The tentorium is readily identified, comprising the entire inner skeleton of the head, fig. 3. For its study it is an easy matter to pick the larger heads to pieces with a needle or to clear the smaller ones in caustic potash and cut off most of one side of the head with scissors.

The tentorium, fig. 3, is composed of the following parts: (1) the corpotentorium (cp), which is the more massive area from which the other parts apparently branch, comprising two lateral plates connected dorsally by a bridge; (2) the metatentorium (mt), which is the part of the corpotentorium adjacent to the metatentorial openings, and which is sometimes continued dorsally and ventro-laterally to form shelf-like metatentorial thickenings; (3) the supratentoria (st), represented by two arms issuing from the anterior or antero-dorsal margin of the corpotentorium and joining the head above or near the antennae; and (4) the pretentoria (pr), two arms extending ventrad or latero-ventrad from the antero-ventral margin of the corpotentorium, often appearing continuous with it, and always provided with mesal, shelf-like processes.

The caudo-cephalic width of the corpotentorial bridge seems to vary considerably within closely allied groups, and therefore may be of little phylogenetic significance. The position and direction of the supratentorial arms, on the other hand, seem to offer characters of some application.

TENTHREDINOIDEA.—*Tenthredo*, fig. 6.—Supratentoria arising at the dorso-anterior margin of corpotentorium and slanting in a dorsal angle to the head capsule. Pretentoria large, appearing confluent with the corpotentorium. Metatentorial thickenings fairly wide, running from the corpotentorium to the dorsal margin of the head. *Cimbex*, fig. 9.—Similar to above, but with the pretentoria very short and stout, undoubtedly an adaption to the extremely strong mandibles and head of the species.

MEGALODONTOIDEA.—*Macroxyela*, figs. 3, 29.—Very similar to Tenthredinoidea.

SIRICOIDEA.—*Xiphydria*, fig. 25.—Supratentoria slender, arising from the anterior part of the corpotentorium, considerably ventrad compared

with their connection in the Tenthredinoidea. Pretentoria more slender than in the Tenthredinoidea, and directed more nearly ventrad. *Tremex*, figs. 30, 31.—Similar to *Xiphydria*, differing in having a longer corpotentorium and a much wider bridge across it. *Orussus*, figs. 26, 27.—Markedly different from any other in the sawflies. Supratentoria short, not reaching the head capsule, their apices needle-like, apparently connected to the head only by a band of muscle. Pretentoria large and thick, directed almost exactly ventrad, their mesal processes large and almost joining on the meson. Corpotentorium short, the bridge very narrow; the supratentoria arising at the antero-dorsal margin.

CEPHOIDEA.—*Janus*, fig. 12.—Similar in many respects to *Xiphydria*. Supratentoria arising simultaneously with the pretentoria from the antero-ventral portion of the corpotentorium; relatively slender. Pretentoria directed almost ventrad, less robust than in the Tenthredinoidea and Megalodontoidea, similar in this respect to *Xiphydria*. Corpotentorium fairly large and long, the bridge wide, and bearing on its anterior margin a small but distinct corpotendon.

ICHNEUMONOIDEA.—Braconidae, *Aleiodes*, figs. 17, 28.—Unlike any of the sawfly tentoria. Supratentoria very long and slender, apparently arising from the pretentoria. Pretentoria long and robust with lateral processes as in the Cephidae; not differentiated from the corpotentorium. Corpotentorium with a narrow bridge from the centre of which arises a prominent corpotendon, furcate at the tip; laterally confluent with the pretentoria.

The Braconid Head

The type of head found in the primitive Braconidae, figs. 10, 11, seems at first glance to be very different from any of the sawfly heads. A study of the essential differences, however, shows that it may be derived from the Cephid head with only a few changes, although these are of quite a revolutionary nature. The evidence offered by other structures is fairly conclusive that the Braconidae originated from a Cephid-like stem, which would therefore demand that the Braconid head be a specialized product of the Cephid head.

The Braconid head differs from that of its progenitor in three important characteristics: (1) the maxillariae (mx) are apparently lengthened to form a gular-like sclerite; (2) the margins of the postgenae and the fused part of the maxillariae are bent back into the head cavity to form a broad shelf upon which the maxillae rest in repose; and (3) the tentorium has assumed the shape shown in fig. 28 with a long corpotendon, long supratentorial arms, and a small corpotentorium. Judging by the relative size and shape of the Braconid and Cephid heads, the former was formed

by a movement and readjustment of parts suggested by the following reconstruction. Starting with the Cephid head, fig. 8, the maxillariae continued to fuse dorsally on the meson, increasing the size of the fused portion and decreasing the size of the occipital foramen. Either subsequent to, or concurrent with, this fusion, the margin of the head around the maxacava (including both postgenae and maxillariae) began bending inward. This continued, increasing the width of the shelf around the maxacava and pushing the metatentorial openings dorsad. Such a series of events would culminate in a head similar in external appearance to that of the Braconidae.

The derivation of the tentorium is not so simple, for the Braconid tentorium is indeed different from the Cephid. The corpotentorium, however, has remained in the middle of the occipital foramen, so that it also must have moved dorsad. In doing so its lateral expanse could easily have been reduced, which would tend to reduce the angle made in the Cephid between the pretentorial arms and the corpotentorium. The large corpotendon is easily explained as an enlargement of the very small one found in the Cephid head. The remainder of the differences will have to be considered simply as readjustments to the new type of head which has evolved.

Labrum

In almost all sawflies the labrum (1) is at least as wide as long, sometimes retracted slightly under the clypeus so that only the anterior margin is visible, figs. 13, 14. The only exception to this is the long, narrow labrum present in the superfamily Siricoidea, figs. 15, 16.

Mandibles

As would naturally be expected with a group of such varied habits, the sawflies exhibit an array of mandibles which is variable in the extreme. From the standpoint of the entire group they are not of great significance in showing relationships. They will, however, undoubtedly prove interesting when more is known of the feeding habits of the adults. A glance at Plates II and III will reveal the diversity found in the group.

Almost all the mandibles have lost the brustiae, prostheca, acia, and a definite mola, and possess only the dentes, or teeth. It is likely that in forms with three or more teeth, figs. 34-36, both proxadentes (px) and distadentes (dx) are represented. In other forms having only two teeth present, figs. 39-41, it is impossible to say whether both or only one of these sets is present. In all cases except the Xyelidae, therefore, these will be referred to simply as teeth.

The lateral aspect of all sawfly mandibles is provided with abundant slender setae, but to date patches of them which correspond to the

brustiae found in more primitive groups have been discovered only in the mandibles of some larval Argidae, fig. 34.

The mandibles of the Xyelidae, fig. 35, are unique in that they possess a larger number of parts than any others in the sawflies. The left mandible has both proxadentes and distadentes differentiated, and a large incised area which has been identified as the mola (ma). The right mandible has the mola very greatly developed into a cusp-like projection which fits into the mola on the left mandible. The brustiae and prostheca are lacking.

The family Tenthredinidae presents a great variety of mandibles, all of which can be traced from a simple, two-toothed form, fig. 51. From this bidentate mandible some have evolved which have lost the inner tooth and become sickle-shaped, figs. 48-50, and others which have developed additional teeth, as shown in figs. 42-44. This is discussed more fully in the treatment of the phylogeny of the Tenthredinidae (see page 61).

The mandibles in some other families have undergone considerable modification. Conspicuous among these are the spatulate, toothless mandibles of the Orussidae, fig. 37, the long, sickle-shaped mandibles of the Pamphiliidae, fig. 4, and those of the Xyelidae, described above.

Maxillae

Except in the family Siricidae, the maxillae of the sawflies, Plate IV, follow essentially a uniform plan. The cardo (cd) is undivided and articulates with the maxillary sclerite. The stipes is sometimes divided longitudinally into the eustipes (eus) and parastipes (ps), in which case the parastipes is always only a narrow, inconspicuous sclerite. The lacinia (lc) is always membranous, sometimes adorned with setae. The galea (gl) is undivided in most forms, but in the Xyelidae, fig. 61, is divided into an ectogalea (ecg) and endogalea (eg). The palpi (p) have from one to six segments. The palpifer is referred to here simply as the first or basal segment of the palpus. The Siricidae, fig. 84, present a case of extreme fusion in which none of the above parts are differentiated except the cardo and palpi.

From the standpoint of phylogeny, the structure of the maxillae offers only incidental help. Two points, however, are of great interest, the similarity of this appendage in the Syntectidae, fig. 70, Xiphydriidae, fig. 69, and Orussidae, fig. 68, and the lack of specialization in the lower Braconids, fig. 67, over the sawfly type.

XYELIDAE.—The two divisions of the galea of the Xyelidae were termed the ectogalea and the endogalea by Crampton (1923). The progressive development of the endogalea, figs. 61, 62, 65, from a constricted

portion of the galea to a long digitate lobe, suggests that these two parts might be homologous to the proxagalea and distagalea found in other insects. The question, however, is entirely open to conjecture; and it seems safest to adopt Crampton's names at present.

Macroxyela, fig. 65.—Cardo short and trapezoidal. Stipes indistinctly divided into eustipes and parastipes, sclerotized on the ventral (ectal) side. Lacinia rounded, clothed with a patch of long setae; apparently continuous with the parastipes. Endogalea a distinct mesal lobe, set with peg-like setae on the mesal margin; ectogalea slightly hooked at the apex, with long setae on the margin. Palpi four-segmented, the last one with a submembranous apex.

Pleroneura, fig. 62.—Lacinia membranous, with an apical row of setae. Galea divided by a furrow into a proximo-lateral ectogalea and a meso-distal endogalea, the latter armed with stout setae.

Xylecia, fig. 61.—Lacinia longer, clavate. Endogalea digitate, long, with a few, scattered, peg-like setae; ectogalea long and relatively slender, with stout setae at the apex.

ARGIDAE.—*Arge*, fig. 63.—Cardo relatively long, folded under the rest of the maxilla in repose. Eustipes large, parastipes very narrow. Lacinia borne at the end of the parastipes, small and triangular, with fine setae on its mesal margin. Galea borne on the eustipes, large and submembranous, with tuft of setae on the ental side. Palpi six-segmented, relatively long and robust.

CIMBICIDAE.—*Trichiosoma*, fig. 64.—Cardo long, folded underneath the remainder of the maxilla in repose. Eustipes large and rectangular, parastipes very narrow. Lacinia almost as large as the galea, with fine setae along the margins. Galea with the basal portion semi-sclerotized, the apical portion forming a rounded, membranous cap bearing a few setae. Palpi scarcely longer than the parastipes, six-segmented, and moderately robust.

These last two maxillae are representative of the group of families contained in the Tenthredinoidea and the family Pamphiliidae. Differences are found in the relative portions of the various segments of the palpi, and the development of the lacinia and galea, but these do not change the fundamental aspect in relation to the other groups.

SYNTECTIDAE.—*Syntexis*, fig. 70.—Cardo small, somewhat trapezoidal. Stipes much as in other groups, the suture dividing it from the parastipes only barely indicated. Lacinia very large, membranous, with a few weak setae at apex; with a crease marking off a relatively wide area along the mesal margin. Galea broadly hook-shaped, submembranous on the latero-ventral side, provided with a brush of stout setae on the meso-dorsal

side. Palpi five-segmented, apparently with little or no articulation between the third and fourth segments; relatively long and moderately slender.

XIPHYDRIIDAE.—*Xiphydria*, fig. 69.—Cardo short, almost square. Stipes much as above, apparently not divided longitudinally into eustipes and parastipes. Lacinia a very weak, rounded, membranous lobe, with only one or two weak setae at apex. Galea much larger, submembranous, covered with fine setae. Palpi five-segmented, short and slender. Judging from the close relationship of this genus with *Syntexis*, the second palpal segment of *Xyphydria* represents the fused second and third of *Syntexis*.

ORUSSIDAE.—*Orussus*, fig. 68.—Cardo short, rectangular. Stipes normal, the parastipes very narrow and separated by a distinct suture from the eustipes. Lacinia a large trapezoidal lobe, entirely membranous and without setae, very much resembling that of *Syntexis*. Galea no larger than the lacinia, membranous on the ventral side, with a thick pad of strong setae on the dorsal side. Palpi about four times the length of stipes, five-segmented, the second segment short, the remainder long, the fifth and the apical portion of the fourth armed with truncate setae.

SIRICIDAE.—*Urocerus*, fig. 84.—Maxillae extremely reduced; the stipes of the two maxillae fused along the mesal line without a suture remaining, so that the two maxillae form a single lunate structure (st). Cardines (cd) also fused on the meson, appearing as two tubercles, each with a thread attached to the basal margin. These threads are attached within the head. Lacinia either atrophied or fused with the galea (gl). Galea continuous with the stipes, the entire appendage uniformly submembranous. Palpi (max. p.) reduced to a single bulbous segment.

CEPHIDAE.—*Cephus*, fig. 66.—Cardo short and trapezoidal. Stipes undivided, normal in general shape; slightly creased at apex to suggest the distal portion of the suture separating the eustipes and parastipes. Lacinia very small, submembranous. Galea large, also submembranous, with a proximo-lateral lobe or fold which appears to form a distinct sclerite. Palpi six-segmented, slightly longer than the stipes.

BRACONIDAE.—*Aleiodes*, fig. 67.—Similar in general plan to *Syntexis*, *Xiphydria*, and *Cephus*. Cardo almost as long as stipes. Stipes undivided, bearing at its distal end the membranous lacinia and the submembranous galea. Galea with a brush of stout setae on its ental side. Palpi six-segmented, four or five times the length of the stipes.

Labium

The various types of labia, Plate V, found in the sawfly groups present a heterogeneous outlay. Most of the differences are due to the relative development of the alaglossa (alg), which is composed of the

fused pair of glossae, and the paraglossae (pgl). The submentum (sm) is usually present, of various sizes and shapes. The mentum is apparently absent. The stipulae (sti) are represented by a sclerotized area basad of or around the palpi and basad of the glossae and paraglossae. The palpi have two, three, or four segments. The paraglossae and the alaglossae are distinct except in the Siricidae, fig. 84, and some Tenthredinoidea (e.g., Loboceridae, fig. 76), in which they all have fused completely to form a totaglossa.

CIMBICIDAE.—*Trichiosoma*, fig. 71.—Submentum elongated, diamond-shaped, separated from the stipulae by a considerable area of membrane. Stipulae bi-emarginate distally forming a median triangle. Palpi four-segmented, the two apical segments provided with sensory areas. Paraglossae large, almost twice the width of the alaglossa, both finely setate on the apical third, the latarima extending to the membranous ligula. Typical of most of the families in the Tenthredinoidea and the family Megalodontidae. In the Blasticotomidae the paraglossae and alaglossa are much reduced but distinct.

LOBOCERIDAE.—*Incalia*, fig. 76.—Differs markedly from the above in having the paraglossae and alaglossa entirely fused to form a totaglossa. This also occurs in *Decameria* (Perreyiidae).

ARGIDAE.—*Arge*, figs. 72, 73.—Submentum and stipulae differing in shape from the above. Stipulae produced mesad to near hypopharynx, somewhat stirrup fashion. Hypopharynx a large sclerotized area with abundant setae. Condition of hypopharynx and stipulae essentially typical of all sawflies with well developed labial parts.

XYELIDAE.—*Macroxyla*, fig. 77.—Submentum shield-shaped, adjacent to the stipulae. Palpi three-segmented, the apical half of the third segment with numerous stout setae. Paraglossae short, with several spine-like setae; alaglossa absent, represented by a membranous area connecting the bases of the paraglossae. In *Megaxyela* the palpi are four-segmented.

CEPHIDAE.—*Janus*, fig. 81.—Stipulae reduced to a narrow, sclerotized band. Palpi four-segmented. Paraglossae lobe-like, only half the width of the alaglossa; alaglossa similarly lobe-like; both of them stumpy and set with thick, small setae and united at the base. Below them is a trapezoidal sclerite (x) set in the apical membranous portion of the stipulae.

XIPHYDRIIDAE.—*Xiphydria*, fig. 82, 83.—Submentum represented by a triangular sclerotized area between the bases of the maxillae, gradually fusing into the membranous area basad of the stipulae. Stipulae with only a narrow, sclerotized basal area. Palpi large, three-segmented, the apical segment with an ovate sensory area. Paraglossae slender, small, and curved, alaglossa broader and more or less truncate at the apex; both

paraglossae and alaglossa very small; the latarima extending basad for the exposed length of the alaglossa.

ORUSSIDAE.—*Orussus*, fig. 80.—Stipulae large, encircling the base of the palpi. Palpi three-segmented, the third segment club-shaped and with curved, strong setae. Paraglossae small, separated from the glossa by sutures, but otherwise not free from it; alaglossa large, with a depressed, membranous, median area; all approaching the condition of a totaglossa.

SIRICIDAE.—*Urocerus*, figs. 84, 85.—Submentum represented by a small sclerotized area between the cardines of the fused maxillae. Stipulae large and shield-shaped, not produced anteriorly into a stirrup-like process. All parts of the glossae united into a totaglossa. Palpi three-segmented, the apical one with a round, membranous, sensory area. Hypopharynx (hy) reduced to a small area of setae, fig. 85.

SYNTECTIDAE.—*Syntexis*, figs. 78, 79.—Submentum ovate, situated in the membrane between the bases of the maxillae. Stipulae large, embracing the bases of the palpi. Palpi three-segmented, the third segment clavate and armed with stout, curved spines similar to those found in the Orussidae. Paraglossae thin and flap-like; alaglossa U-shaped, encircling the paraglossae at their base, these latter being situated within the circle of the alaglossa and covering most of it from view when seen from the posterior aspect. The alaglossa of this species might superficially be termed a "duplaglossa," which has previously been considered as restricted to the higher Hymenoptera. It is very similar to that found in the Braconidae (see *Aleiodes*, fig. 75), having similar rows of microtrichiae on the anterior face. It differs slightly from the true duplaglossae, however, in that the paraglossae are contained within the hollow semi-circle formed by the alaglossa instead of being situated beside it.

BRACONIDAE.—*Aleiodes*, figs. 74, 75.—Stipulae large, similar in type to that found in sawflies. Palpi four-segmented. Paraglossae small, reduced to flaps along the base of the duplaglossa. Duplaglossa large, somewhat V-shaped, bearing rows of microtrichiae on the anterior surface.

The trend of development in these labia has been one leading from a condition in which the paraglossae were large and the alaglossa subordinate to them, to one reversing this relation, having the alaglossa large and the paraglossae subordinate to it. This has led to the totaglossa of the Siricidae, Loboceridae, and Perreyiidae on the one hand and the duplaglossa of the Apocrita on the other.

Antennae

The antennae, figs. 86-107, vary greatly both in shape and the number of segments comprising them. They are frequently of use in the diagnosis

of genera or larger groups, and undoubtedly offer some of the best characters for keying out the families. They apparently afford few clues as to the phylogeny of the various sawfly groups. There is no gradual development towards a predominant type as, for example, the case of the aristate antennae of the cyclorrhaphous Diptera. They will be discussed, therefore, simply according to shape.

Filiform and setaceous.—This is the common type found in most of the sawflies. The number of segments may vary from six in the Acorduleceridae, fig. 95, to thirty or more in the Pamphiliidae, fig. 88. An interesting deviation from the setaceous type is found in the Argidae, Xyelidae, and Blasticotomidae. The third segment has become greatly lengthened and thickened, and the remaining apical segments are either absent (Argidae, fig. 97), reduced to a small stub (Blasticotomidae, fig. 96) or form a slender, segmented filament (Xyelidae, figs. 86, 87).

Furcate.—The males of some genera of the Argidae have undergone a further modification of the enlarged third segment, which is divided longitudinally for almost its entire length, forming two slender filaments which are usually somewhat curled and harp-shaped, fig. 98.

Fusiform.—Some species of *Macrophya*, fig. 103, and the females of *Orussus*, fig. 92, have the preapical segments enlarged, giving it a decided spindle shape.

Serrate.—In those families in which setaceous or filiform antennae are the rule, occasionally genera appear in which the antennae are more or less distinctly serrate. In some Diprionid genera, e.g., *Augomonoctenus*, fig. 107, and *Monoctenus*, the female antennae are markedly serrate. In some Tenthredinidae, e.g., *Ceratulus*, fig. 355, both sexes have serrate antennae.

Pectinate.—The males of Diprionidae, fig. 105, the genus *Pterygophorus* and the genus *Cladius* (Tenthredinidae), fig. 104, have antennae which are very conspicuously pectinate. The females associated with these may have the antennae either setaceous, serrate, or pectinate, but in the latter case, fig. 106, never to the same extent as the males.

Flabellate.—The males of *Megalodonta* have curious antennae, fig. 94. The segments of the flagellum are provided with distinct lamellae which are small and ovate, and may be folded back in repose so that the antenna appears filiform.

Clavate.—The Pergidae and some groups of the genus *Tenthredo*, figs. 101, 102, of the family Tenthredinidae have antennae with a well-formed, but not conspicuous club.

Capitate.—In the Cimbicidae the club is large and the "handle" (third segment) is very slender, fig. 100.

THORAX AND APPENDAGES

Since the thorax of sawflies has been studied in comparison with that of the Apocrita and other orders by Snodgrass (1911), only those parts will be mentioned in this discussion which have shown differences of taxonomic or phylogenetic significance within the sawfly groups. These consist chiefly of the cervical sclerites, mesonotum, and mesopostnotum.

Cervical Sclerites

Crampton's interpretation of these sclerites is adopted here. This postulates, fig. 146, that the large, lateral sclerites (cv) lying antero-dorsad of the prosternum represent the enlarged cervical sclerites to which are fused the reduced propleurae (pl). In the Tenthredinoidea the propleurae are usually demarked by a suture, but even in some of these forms it is almost impossible to be sure of these sutures.

In most of the Tenthredinoidea the ventro-mesal portion of the cervical sclerites is V-shaped or U-shaped, not meeting on the meson, figs. 155, 156. In other members of the superfamily, the sclerites practically meet on the meson, and the ventro-mesal margin is truncate, figs. 157, 158, or subtruncate, fig. 154. This enlargement and strengthening appears to be purely adaptive and a modification very easily acquired. Thus, in the family Tenthredinidae these sclerites have become truncate and approximate on the meson in the subfamilies Tenthredininae, Dolerinae, and Allantinae. The primitive genera of the Tenthredininae and Allantinae have these sclerites unmodified, so that the development of these truncate sclerites has occurred independently in each of the three subfamilies mentioned.

In the Cimbicidae, fig. 159, an interesting modification occurs. The lateral angles of the prosternum unite with the mesal margin of the cervical sclerites to form a precoxal bridge. This, however, is not the primitive condition typical of the sawflies, but simply an aberrant offshoot.

In the Siricoidea, figs. 132, 133, and Cephoidea, fig. 131, the cervical sclerites are very large, with the ventro-mesal margins truncate and more approximate than in any of the Tenthredinoidea. This is the condition typical of the Apocrita.

Propleurae

The propleurae are either separated from the cervical sclerites by a distinct suture, or undifferentiated, in which case they form the posterior portion of the cervical sclerites. In the Xyelidae, fig. 148, they are extremely small and difficult to differentiate. In the Tenthredinoidea, fig. 146, and some Siricoidea, fig. 147, they are longer, and are almost entirely invaginated into the body, giving an apodeme-like appearance.

The study of this structure, however, is at present not extensive enough to be used as a basis for any conclusions.

According to Crampton (1926), the propleurae are divided by a distinct suture into the episternum and epimeron, but I have not yet been able to observe this suture. The line of origin of the propleurodeme is difficult to determine exactly, and may be the suture here considered to separate the cervical sclerites and the propleurae. When this and some other uncertain points are finally cleared up, our conception of the homologies of this region may have to be modified.

The "Atlas"

The cervical sclerites, fig. 129, cv plus bs, (including the fused propleurae) and the probasisternum together from a single unit from the standpoint of function. The head articulates at the anterior end of the cervical sclerites, the prothoracic legs between the basisternum and procoxacondyle. The cervical sclerites and prosternum are firmly united by means of the strong endoskeleton, but are united to the remainder of the body only by membrane. Consequently, the head and front legs have not only their articulation where they join the cervicum and prothorax, but in addition the flexibility allowed by the membranous connection of these parts. For this combination of cervical sclerites and probasisternum the term "atlas" is proposed, since it is analogous to this structure in the vertebrate skeleton.

Prosternum

The prosternum is primitively represented by two widely separated sclerites, fig. 129, the basisternum (bs) and the spinisternum (ss). The basisternum is between and sometimes partly under the mesal portion of the cervical sclerites, and between the front legs. It is variable in shape, being diamond-shaped, ovate, T-shaped, or I-shaped; internally it bears the large, fused furca.

An unrecorded sclerite, the spinisternum.—The spinisternum (ss), if differentiated as a distinct sclerite, is situated on the meson just anterior to the mesosternum or mesopleurae. It is a small sclerite and usually bears internally a small furcella or plate, fig. 153 (fl). In the Megalodontoidea, some of the families of the Tenthredinoidea (e.g., Argidae, fig. 134) and the Siricidae, fig. 138, it is distinct, but in this last family lacks the furcella. In the Syntectidae, Xiphydriidae, and Cephidae the spinisternum is represented by a very small, indistinct thickening of the membrane only. In the higher Tenthredinoidea, fig. 136, it is apparently fused with the mesosternum and forms the small triangular area between the anterior fork of the mesofurcina.

Mesosternum

In many sawflies this area is distinct, separated from the mesepisterna by well-marked sterno-pleural sutures. In others it may be entirely fused with them, or at the most separated by obsolescent sutures. There is a deep suture along the meson which marks the emargination of the fused and lengthened furca, fig. 153, (fc).

XYELIDAE AND PAMPHILIIDAE, fig. 129.—Sternum (ms) forming a triangular area, divided from the episterna by a distinct or at least a well-marked suture; episterna (eps) produced mesally and fused anterior to the sternum to form a wide presternal bridge (psb).

CEPHOIDEA, fig. 131.—Sternum triangular, longer than in the above, the sterno-pleural sutures converging and meeting near the anterior margin of the segment. Presternal bridge very narrow, not distinctly differentiated from the antecostal ridge of the sclerites.

SIRICOIDEA.—Syntectidae, fig. 130.—Sternum more or less short and triangular, set off from the episterna by distinct sutures terminating anteriorly on the meson in deep pits. Episterna bilobed anteriorly, the three incisions between the lobes membranous. Furcal suture extending to the anterior margin of the segment, apparently representing a narrow tongue of the sternum separating the two episterna. The condition is peculiar, apparently most resembling the Pamphiliid type, fig. 129.

XIPHYDRIIDAE, fig. 132, AND SIRICIDAE, figs. 137, 138.—Sternum fused with episterna with no evident suture. In these two families, however, the furca does not quite reach the anterior margin of the segment, indicating the presence of a narrow presternal bridge. Furthermore, there is a triangular area, fig. 138, (ms), separated from the lateral areas by a convexity, by slight differences in texture and by a lack of large punctures. This area may be regarded with certainty as the true sternal region.

ORUSSIDAE, fig. 133.—In this family also the sternum is fused with the episterna with no distinct suture between them. There are, however, faint remnants of the sterno-pleural sutures in the form of impressions on the external surface of the sclerites. When traced out these delineate a triangular sternum, the tip of which just reaches the anterior margin of the segment.

TENTHREDINOIDEA AND MEGALODONTIDAE, fig. 134.—Sternum trapezoidal, episterna well separated anteriorly, not forming a presternal bridge. This condition is present in the Pergidae, Pterygophoridae, Loboceridae, Perreyiidae, and some genera of the Argidae, fig. 134. In other Argidae and the Cimbicidae the sterno-pleural suture is weak or entirely absent, as is the case with all the remaining Tenthredinoidea, figs. 135, 136. In these latter, however, it is a simple matter to demonstrate that they

are a derivative of the trapezoidal type of sternum, since the path of the sterno-pleural suture is indicated as in fig. 134 by lines of punctures, color differences, depressions in the surface of the sclerite, and a distinct internal line of muscle attachment.

Pronotum

This sclerite is quite varied in shape. In the Xyelidae, fig. 120, (pn), Cephidae, fig. 121, and Syntectidae, fig. 122, it is somewhat rectangular, and slightly narrowed on the meson; in the Xiphydriidae, figs. 123, 141, Siricidae, fig. 127, and Orussidae, figs. 128, 142, it is of approximately the same dimensions but tilted forward into a vertical position. In the Tenthredinoidea, figs. 124, 139, it is greatly reduced on the meson, forming only a narrow collar at this point.

Mesonotum

The sawfly mesonotum, fig. 120 (II), is primitively divided into four major parts—praescutum (prs) subdivided on the meson into two lateral halves, scutum (scut), scutellum (scl), and postnotum (ptn), most of which is invaginated underneath the metanotum. The postero-lateral areas of the scutum are usually markedly declivous, forming the parascutellar areas (is). Some groups have an apparent posterior lobe of the scutellum, the post-tergite (pt). All the sclerites are subject to variation, which may be discussed to best advantage according to taxonomic units.

MEGALODONTOIDEA, fig. 120.—Praescutum diamond-shaped; scutum large, not divided transversely; scutellum V-shaped anteriorly; the posterior margin of the scutellum produced into a narrow post-tergite (pt); postnotum forming the lateral post-alar bridge, and forming a phragma underneath the metanotum. The phragma, fig. 149, is about two-thirds concealed, the concealed portion consisting of two small lateral lobes and two large median lobes.

TENTHREDINOIDEA, figs. 124, 126.—Similar to the Megalodontoidea. Post-tergite absent in all but the Diprionidae, in which it is only a narrow cord, and the Tenthredinidae, in which it is usually well-developed and triangular, figs. 124, 125. The Acorduleceridae, fig. 126, are unique among the Tenthredinoidea in having the lateral and mesal sutures of the praescutum distinct only for the anterior two-thirds of their length, so that the praescutum is not separated from the scutum which therefore appears much longer than normally; and in having the scutellum transversely sinuate on its anterior margin. Throughout the Tenthredinoidea the postnotum is similar to that of the Megalodontoidea.

CEPHOIDEA, fig. 121.—Similar to the Megalodontoidea, except as follows: post-tergite very small, scarcely present; postnotum, fig. 152, very

long, much narrower, with the two small, lateral lobes considerably reduced; parascutellar areas not distinctly set off from the scutum.

SIRICOIDEA.—The Syntectidae, fig. 122, are similar to the Cephidae, fig. 121, (condition of the postnotum unknown). The remainder of the Siricoid families differ considerably from this primitive type.

Xiphydriidae, fig. 123.—Scutum divided by a transverse suture near its middle into anterior and posterior halves. Praescutal sutures extending meso-caudad to this trans-scutal suture, so that the praescutum is much longer than normally. Parascutellar areas relatively distinct. Scutellum differentiated anteriorly and laterally by broad, trench-like sutures. Postnotum as in the Megalodontoidea, fig. 149.

Orussidae, fig. 128.—Scutum divided transversely. Praescutal sutures extending almost longitudinally from the pronotum to the trans-scutal suture; the median praescutal suture absent, so that the praescutum is an undivided, rectangular sclerite. Scutellum distinctly set off by sutures; the scutum apparently solidly united to the postnotum so that the scutellum appears to be surrounded by the scutum. Postnotum longer than in the Xiphydriidae, fig. 150.

Siricidae, fig. 127.—Scutum divided by diagonal, wide, trench-like sutures into an anterior sclerite and two postero-lateral sclerites (y). Praescutal sutures present only as faint traces, the praescutum therefore appearing fused with the anterior sclerite of the scutum. Postnotum considerably lengthened, fig. 151.

Metanotum

In the Megalodontoidea, fig. 120 (III), Tenthredinoidea, and the family Syntectidae of the Siricoidea, fig. 122, the metanotum is separated from the mesonotum by a deep furrow marking the invagination of the postnotum. In these the scutum and scutellum may be fairly readily identified, figs. 120, 122. In addition to these areas, a pair of hard, opaque, rough areas are present on the scutum, known taxonomically as the cenchri (cn). The praescutum is either absent or undifferentiated. The two chief differences from this condition may be briefly summarized as follows: (1) in the Cephidae, fig. 121, Xiphydriidae, fig. 123, Siricidae and Orussidae, fig. 128, the metanotum is closely appressed to the posterior margin of the mesonotum, and part of the metascutum is hidden from view; in the last three families named, the cenchri appear as small pads protruding from the suture formed by this consolidation; (2) in the Cephidae the cenchri are entirely wanting. The scutellum also is more or less undifferentiated in the families mentioned above.

Mesopleurae

A hypothetical sawfly mesopleuron would be as follows: prepectus

present as a distinct sclerite, fig. 129, (pp); pleural suture present, dividing the pleuron into the mesoepisternum and mesoepimeron; epimeron divided by a short epimeral suture into the anepimeron (aem) and katepimeron (cem). Unlike the epimeron, the episternum is never divided. The deviations from this type are primarily due to the atrophy of one or more of the sutures.

TENTHREDINOIDEA, fig. 139.—Prepectus either present or absent, sometimes the two conditions being found in closely related genera. In some cases the prepectal suture is modified into a furrow and the prepectus is present as a shoulder-like ridge. Pleural suture present. Epimeron divided; anepimeron markedly convex, katepimeron usually flat, the epimeral suture dividing them sometimes obsolete but the two parts distinct due to their great difference in convexity.

MEGALODONTOIDEA.—Similar to above, differing in having the epimeron undivided.

SIRICOIDEA AND CEPHOIDEA, figs. 140-143.—In these two superfamilies the epimeron is undivided as in the Megalodontoidea. The pleural suture is either lost or indistinct in most of these families, frequently discernible only at one end.

Metapleurae

Similar in general features to the mesopleurae, differing, however, in lacking a prepectus and having the sutures disappear in this segment before they do in the mesopleurae. An interesting modification occurs in the Pergidae and Philomastiginae. The metaepimeron is not only undivided but solidly fused with the lateral margin of the first abdominal tergite. Intermediates between this and the free condition are found in the Perreyiinae and to some extent in other members of the Tenthredinoidea.

Legs

The three pairs of legs are built essentially along the same plan, consisting of the following parts, fig. 110—coxa (cx), two-segmented trochanter (tr), femur (fm), tibia (tb), five-segmented tarsus (ta), and tarsal claws (tc). The only known exception to this is the front leg of the female of *Orussus*, fig. 108, which has the apical portion of the tibia constricted to form an additional tibial segment and has only four segments to the tarsus, the first segment hidden in the distal end of the tibia so that the tarsus appears three-segmented.

The tibial spurs present several characters worthy of note. Preapical spurs, fig. 110, (psp), numbering from one to four, are present on the middle and hind legs of the Pergidae, Acorduleceridae, the genus *Arge* in the family Argidae, and the families Xyelidae, Megalodontidae,

and Cephidae. The front tibia of the genus *Acantholyda* (Pamphiliidae) also has a pre-apical spur. Occasionally one is found on the middle or hind tibiae of the Loboceridae, and may likely appear haphazardly in other groups.

All the tibiae are provided with one or two apical spurs, fig. 110, (asp). On the middle and hind tibiae they are quite uniform, but on the front tibiae offer some valuable differences as follows. In the Pergidae, Acorduleceridae, Argidae, Pterygophoridae, Cimbicidae, Diprionidae, Perreyiidae, and Loboceridae two are present, both of the same shape, although one may be slightly smaller than the other, fig. 113, (asp). Usually they are pointed but in some genera may be truncate or even slightly swollen at the apex. In the Tenthredinidae, Blasticotomidae, Xyelidae, Megalodontidae, and Orussidae, two apical spurs are present, but one is broadened and branched or incised at its tip, fig. 114. In the Orussidae the unbranched spur is very small, fig. 115. In the remainder of the sawflies, the Cephidae, Syntectidae, Xiphydriidae, and Siricidae, the unbranched spur has been lost entirely, and the modified spur has developed into several different forms. That of *Xiphydria*, fig. 117, is long and slender, similar to that of *Orussus*. In the Siricidae, fig. 116, the spur has widened, and the inner side is sub-membranous. In *Syntexis*, fig. 118, the inner margin has become transversely incised to form a pectinate fringe running almost the entire length of the spur, and the outer tooth of the apical incision is small and slender. In the Cephidae, fig. 119, this outer tooth is very large, the inner one being small.

In some genera of the Siricidae, the middle and hind tibiae have only one apical spur.

Wings

The multitude of differences found in the venation of sawfly wings has been the basis for several methods of classifying the groups themselves. When, however, the wings are studied after the other parts of the insect, two facts are apparent: (1) the characters of the venation give assistance in tracing evolution in only a few cases, and (2) parallel evolution has occurred in many instances.

The systems of nomenclature for the Hymenopterous wing are many. These have been discussed in a previous paper (Ross, 1936a) and the system there propounded is used here. The simple evolution of the Hymenopterous venation from the Panorpid types is the basis for the terminology, which is given in figs. 170 and 211.

The most primitive characters in the sawfly wings are: (1) a free subcosta in the Xyelidae and Pamphiliidae, fig. 172; (2) the unfused condition of media and radial sector, which are therefore separated by the first radio-medial cross-vein, in *Pleroneura*, fig. 172; (3) the presence

of the base of all the anal veins in some Siricidae, fig. 173; and (4) the presence of the base of cubitus in the hind wings of some Xyelidae, much as in fig. 170.

The most marked differences between the superfamilies include: (1) the unique tendency in the Tenthredinoidea for continued basal fusion of media along radial sector, this fusion frequently going back down the stem of radius, fig. 185; (2) the partial loss of the first radial cross-vein in some Cephidae and its total atrophy in the Orussidae; and (3) the more or less straight course of the veins in the Siricoidea and Cephioidea.

Parallel development has taken place most frequently in the anal veins. There seems to be a tendency in all sawflies for 2A & 3A to fuse with the first anal vein. It has occurred in the Argidae, Diprionidae, and Cimbicidae and is very well illustrated in the Tenthredinidae, figs. 197-210 (see p. 61).

There seems to be little uniformity in the atrophy of veins or cross-veins. In many cases the atrophy of a portion of the venation may be simply individual variation, and in other cases it may typify species or genera. The only family in which the venation shows consecutive steps in variation is the Tenthredinidae, under which heading it is discussed fully.

ABDOMEN AND APPENDAGES

As with the thorax, the general features of the sawfly abdomen have been studied by Snodgrass (1931). Only those parts will be discussed here, therefore, which have some bearing on the question of relationships.

First Abdominal Tergum, or Propodeum

The first segment is represented only by the tergum, the sternum being either membranous or atrophied. This first tergum is an integral part of the metathorax, since it is fused quite solidly with it in all sawflies. If the body is broken, the break occurs between the mesothorax and metathorax, not between the thorax and abdomen. The first tergite, fig. 120, (1), is typically divided or incised on the meson, to produce two lateral plates. These are referred to in taxonomic literature as the "basal plates" or "propodeum." In some genera or families (e.g., Orussidae, Cimbicidae, and some Tenthredinidae), they have become reunited, fig. 128.

In most sawflies the dorsal contour line of the metathorax and the first two abdominal terga, when viewed laterally, is almost continuous, without marked constrictions between the segments, figs. 139, 140, 142. There are only two distinct exceptions to this: (1) the Xiphydriidae, fig. 141, have a distinct constriction between the metanotum and first tergite; and

(2) the Cephidae, fig. 143, have a very well marked constriction between the first and second tergites. In the Apocrita, fig. 144, the first tergite is entirely fused with the metanotum, and the second and following segments articulate with the first by a ball-and-socket joint. While no such joint as this exists in the Cephidae, the articulation of the rest of the abdomen does occur at this point, and there is a suggestion of a joint at the postero-lateral angle of the first tergite.

Male Genitalia

The terminology advocated by Crampton (1919) has been used for the parts of the male genital capsule, for the reason that it is the only one taking into account the prior use of names for some other part of an insect. For instance, the terms "cardo," "stipes," and "manubria," used by some authors for parts of the genitalia, are in current usage for sclerites of mouthparts or other appendages, and these Crampton has changed or discarded. His argument is quite sound that this is the only way to arrive eventually at a uniform and nonconfusing terminology of homologous parts of different insects.

The male genitalia, as would be expected, present a multitude of differences, especially in the Tenthredinoidea. As far as can be ascertained at present, a great deal of this variation is of use only in grouping related genera. Only a few of the differences show relationships between larger groups, and these are the differences discussed here.

The genitalia present two different orientations. In one group the adult genital capsule remains in the same orientation as in the pupa. In the other the capsule revolves through a 180° angle around its linear axis. This was first pointed out by Crampton (1919), and was later shown by Boulonge (1924) to occur just prior to eclosion. Crampton proposed the terms "Orthandria" for those sawflies with normal genitalia and "Strophandria" for those in which the genitalia turned. The latter includes only the Tenthredinoidea, while the former includes the Megalodontoidea, Siricoidea, and Cephioidea.

The genital capsule, fig. 160, is composed of the following sclerites: (1) gonocardo, or basal ring (ca); (2) a pair of gonostipites, (go), comprising the lateral foundation; (3) harpes (h), or appendages of the gonostipites; (4) sagittae (sa) and volsellae (ol); two pairs of sclerotized plates, primitively ventral, but dorsal in the Strophandria or Tenthredinoidea; (5) a pair of penis valves (py), enclosing the true penis; and other structures of a sporadic nature, including the gonamaculae (gm) or apical muscular disc of the harpes of the Megalodontoidea and others, the parapenes (gg) of some Tenthredinoidea, and the median sclerotized style of the Siricidae and Cephidae.

TENTHREDINOIDEA.—*Arge*, fig. 160, *Trichiosoma*, fig. 163, and *Acordulecera*, fig. 164.—Genitalia are turned so that the volsellae and sagittae are on the dorsal surface. Gonocardo usually present, sometimes partially atrophied. Gonostipites present, varying in form; in the Cimbicidae and Tenthredinidae incised on the ventral surface to form a pair of median lobes or processes, the parapenes. Harpes always present, articulating with the gonostipites; never with gonomaculae. Volsellae and sagittae always approximately the same shape; sagittae with a mesal hook-like process and an apical point or process. Penis valves of many different shapes. They are characters which are extremely valuable in specific diagnosis of many genera.

MEGALODONTOIDEA.—*Macroxyela*, fig. 167.—Capsule not turned, the sagittae and volsellae on the ventral surface. Gonocardo present as a broad band. Gonostipes large, resembling in shape that found in *Arge*, fig. 160. Harpes articulating with the gonostipes, with an apical gonomacula (gm). Volsellae and sagittae similar to those of Tenthredinoidea, but much reduced. The genitalia of the Megalodontidae are similar in all essentials to those of the Xyelidae with the exception of the gonocardo, which is very narrow, and the volsellae and sagittae which are even further reduced.

SIRICOIDEA.—The genitalia of the families of this group differ greatly, so they are described separately.

Xiphydriidae (*Xiphydria*, figs. 161, 162).—Very similar to *Macroxyela*, differing only slightly in the relative size of the parts. Volsellae and sagittae essentially like those of *Macroxyela*, fig. 167, small, and concealed on the mesal face in repose. Harpes with gonomaculae.

Siricidae (*Urocerus*, fig. 166).—Dorsal expanse of gonostipites larger, ventral expanse smaller than in *Xiphydria*. Harpes stout, with gonomaculae. Volsellae represented by a flat, sclerotized plate. Sagittae more erect in position, the apical portion rounded and bearing tooth-like projections. Penis valves stouter. Ventral surface with a long, slender, sclerotized style extending from the base up the meson of the gonostipes to the base of the sagittae.

Orussidae (*Orussus*, fig. 169).—Very unlike the capsule of any other sawfly. Gonocardo large, wide on the dorsum. Gonostipes with a large dorsal expanse, fused on the center with the volsellae, the two separated by a suture. Sagittae greatly elongated, with a long basal portion and an apical, clasper-like portion which extends slightly beyond the harpes. Harpes separated from the gonostipes by a wide area of membrane, triangular, and more or less inconspicuous due to the larger apex of the sagitta; gonomaculae not present.

CEPHOIDEA.—The genitalia of the only family in the superfamily show some interesting deviations from other sawfly capsules. *Janus*, fig. 165.—Gonocardo enlarged laterally to form a very thin sheath covering the basal portion of the gonostipes. Gonostipes and harpes separated either by an indistinct suture or not at all, with no articulation between the two sclerites. Volsellae and sagittae with their apices knob-like and provided with minute peg-like elevations.

ICHNEUMONOIDEA.—Braconidae (*Aleiodes*, fig. 168).—Considerably different in aspect to any of the sawfly genitalia except those of the Cephidae, fig. 164. Gonocardo ring-like, as in the sawflies. Gonostipes and harpes completely fused with no trace of a dividing suture. Sagittae similar in shape and position to those of *Janus* and *Urocetus*. Volsellae large, the apical portion triangular. Both volsellae and sagittae provided with small knobs or teeth at apex. The genitalia of several other Ichneumonoids have been examined and found to be of the same type as *Aleiodes*, the sagittae and volsellae occupying approximately the same position, and the harpes always completely fused with the gonostipites.

A restudy of the male genitalia has substantiated practically all the conclusions pointed out by Crampton. They show that the Megalodontidae and Xiphydriidae are closely related, and that the former are similar in many respects to the Tenthredinoidea. One point is especially noteworthy. The almost complete fusion of the harpes with the gonostipes in the Cephidae is a distinct step towards the condition found in the Ichneumonoidea, which rebuts as much as anything else the assertion of Rohwer and Cushman that the Orussidae are the true intermediates between the Symphyta and the Apocrita. It is quite evident from the male genitalia that the Cephidae are the true intermediates between these two suborders.

PHYLOGENY

In a review of the morphology, three sets of characters stand out as offering a basis for primary groupings of the sawflies. These are:

(1) Head capsule, with its four types:—open, fig. 2; maxapontal, fig. 8; genapontal, fig. 19; and closed, fig. 5.

(2) Mesosternum, with its three types:—trapezoidal, fig. 134, and its derivatives through atrophy; triangular, without a wide presternal bridge, fig. 131; and triangular, with a wide presternal bridge in front of it, fig. 129.

(3) Male genitalia, with two types:—normal, with the sagittae and volsellae ventral in position; and turned so that the sagittae and volsellae are dorsal.

THE SUPERFAMILIES OF SAWFLIES

Trial and error grouping on the basis of the above characters shows that any one set does not give satisfactory division. For instance, if we group together all those with the open type of head, we find forms with the trapezoidal sternum and inverted genitalia included among those with the widest presternal bridge and normal genitalia. There are so few discrepancies of this nature, however, that continued experimental groupings bring out the existence of four major divisions of the sawflies, which are considered superfamilies, as follows:

Tenthredinoidea.—This group is unique in having the male genitalia inverted, the pronotum narrow and reduced to a thin strap on the meson, and in combining an open type head with a trapezoidal mesosternum, whether determined by sutures or internal muscle attachments. These two latter characters are not confined to this superfamily but are found together in no other.

Siricoidea.—Set off from all other sawflies by the genapontal head, fig. 19, and spatulate labrum, fig. 15. As nearly as can be determined the sternum is triangular, with definite evidence of a narrow presternal bridge in some forms. This is undoubtedly the most heterogeneous group of the sawflies.

Cephoidea.—This small superfamily is characterized by the maxapontal head, fig. 8, and a large number of other characters not possessed by other sawflies. These include such significant items as: (1) possession of a corpotendon on the tentorium, fig. 12, as well as the apical origin of the supratentorial arms; (2) lack of well differentiated claspers in the male genitalia, fig. 165; and (3) lack of cenchri, fig. 121.

Megalodontoidea.—Three families, Xyelidae, Pamphiliidae, and Megalodontidae, have been placed together in this superfamily. They combine

an odd assortment of extremely diverse characters. The Xyelidae have an open type head, fig. 2, and a wide presternal bridge, fig. 129. The Pamphiliidae have the extreme closed head, fig. 5, but in almost all other respects are similar to the Xyelidae, including the wide presternal bridge. The Megalodontidae also have the closed head and in most characters are similar to the Pamphiliidae but lack all trace of a presternal bridge, in fact have a trapezoidal mesosternum as have the Tenthredinoidea.

FAMILY GROUPINGS

Tenthredinoidea

The members of this superfamily have extremely diverse antennae and wings. The antennae include such extreme types as bifurcate, fig. 98, pectinate, fig. 105, serrate, fig. 106, clavate, fig. 101, capitate, fig. 100, and various proportions of simple types, figs. 93, 97. The wings vary in the position of almost any vein or cross-vein, and the shape of almost any cell.

Grouping characters of a more fundamental nature include the presence or absence of (1) preapical spurs on the tibiae, (2) sterno-pleural sutures, and (3) parapenes on the male genitalia, fig. 163. Intergrading forms occur between the extremes of the latter two.

By using characters distinctive to a single group it is possible to break up the nearctic representatives into five families, as follows:

Argidae.—Antennae three-segmented, the third segment long, either simple, fig. 97, or furcate, fig. 98.

Acorduleceridae.—Praescutal sutures atrophied posteriorly, and anterior margin of mesoscutellum sinuate, fig. 126. Antennae six-segmented, small, fig. 95.

Tenthredinidae.—Inner spur of front tibiae cleft at apex, fig. 114. Antennae have eight to ten segments, ranging from filiform to clavate; sometimes with one or two pectinations, fig. 104. Sterno-pleural sutures and preapical spurs absent.

Diprionidae.—Antennae serrate, fig. 107, or pectinate, fig. 105, having at least twelve segments. Sterno-pleural sutures and preapical spurs absent.

Cimbicidae.—Lateral margins of abdomen sharply angled. Antennae capitate, fig. 100. Sterno-pleural sutures and preapical spurs absent.

The Australian and South American faunas contain a large number of forms which are divided by Rohwer and Benson into three or four families, the Pergidae, Loboceridae, Perreyiidae, and Pterygophoridae. These are apparently close relatives of the Argidae and Acorduleceridae, having either preapical spines on the tibiae, sterno-pleural sutures, or the simple

type of male genitalia without parapenes. A detailed study of this fauna, especially from the neotropical regions, is necessary before the segregation of these groups can be stabilized.

Megalodontoidea

The head capsules at once divide the nearctic members of this superfamily into two groups, those with an open head, fig. 2, and those with the closed head, fig. 5. Within these two groups there are a few striking differences, so they are considered two families, viz.:

Xyelidae.—Head capsule open, fig. 2. Antennae with third segment greatly lengthened or enlarged, figs. 86, 87. Labium with alaglossa absent, fig. 77.

Pamphiliidae.—Head capsule closed, fig. 5. Antennae filiform, fig. 88. Labium with alaglossa present, as in fig. 71.

Siricoidea

Of the four superfamilies, the Siricoidea is divisible into the best marked families. The diverse types of mesonotum, mesosternum, mouthparts, etc., indicate the existence of four families, as follows:

Syntectidae.—Mesosternum triangular, fig. 130, with the mesopleurae produced to form two long, rounded processes in front of it. Mesonotum without a transverse suture, but normally divided, fig. 122; head without a groove for the reception of the antennae in repose, fig. 21.

Xiphydriidae.—Mesosternum with sterno-pleural sutures almost atrophied; mesonotum divided by a transverse suture, otherwise normally divided, fig. 123; head with a shallow groove for reception of antennae, fig. 22.

Siricidae.—Mesosternum set off from pleurae as a depressed area, fig. 138, with a narrow presternal bridge, fig. 137; mesonotum with praescutal sutures faint, and with two lateral grooves setting off parascutal lobes, fig. 127 (y); head with narrow, reniform eyes and a well marked antennal groove, fig. 18.

Orussidae.—A very striking group set off by the head, in which the portion bearing the antennal sockets, pretentorinae, clypeus, and labrum has shifted on to the ventral aspect, figs. 23 and 24, with a curiously modified tentorium, figs. 26 and 27.

HYPOTHESIS OF GENEALOGY

The evolutionary tendency of the sawfly groups (and Hymenoptera) has been chiefly in the direction of fusion or simplification of parts. The

wing venation and the thoracic sclerites, for instance, have been greatly reduced in number of parts in comparison with the Neuropterous types, from one of which they undoubtedly arose (Ross, 1936a). This, however, is not a uniform rule for modifications within the order. Evolution may be expressed equally well by the addition of parts as well as their subtraction. A good example of this is seen in the case of the mandibles in the family Tenthredinidae (Plate III). The four-toothed mandible of *Tenthredo*, fig. 42, and the one-toothed mandible of *Eriocampa*, fig. 48, both have developed from the bidentate type represented by *Lycaota* and *Strongylogaster*, figs. 46, 51, the former by the addition, the latter by the reduction, of parts. The same is shown by the antennae, the simple, nine-segmented antenna of the Tenthredinidae, fig. 103, having arisen from the same stock as the multi-segmented pectinate antenna of the Diprionidae, fig. 105. The condition of the antenna of the Tenthredinidae has resulted from a reduction in the number of segments and the lengthening of each segment; that of the Diprionidae from the addition of lateral outgrowths to a more or less primitive multi-segmented antenna.

The entire sawfly group is relatively closely knit from a structural basis, when one considers the resemblance of primitive forms of each superfamily. A conclusion based on the extremes in structure between distantly related forms would be very different, but such a conclusion is one-sided and erroneous. In fact, so small is the jump between any two related families that it seems very advisable to consider the group as a single suborder, the Symphyta.

The Symphyta are divisible into two major series, the Strophandria (Tenthredinoidea) and Orthandria (Megalodontoidea, Siricoidea, and Cephioidea). The Strophandria are characterized as follows: male genitalia turned 180° on the median axis before eclosion; and second radial cross-vein (if present) joins R_2 distad of the second radio-medial cross-vein. In the Orthandria the male genitalia are not turned and the front wings have second radial cross-vein joined to R_2 proximad of the second radio-medial cross-vein. The Strophandria comprise a compact group, and the Orthandria contain a series of superfamilies which are closely linked by their respective primitive families, the Xyelidae, Syntectidae, and Cephidae.

The Strophandria have undergone considerable modification of antennae, tibial spurs, wing venation, and mouthparts, and have lost certain sutures in some families, for instance the sterno-pleural and prepectal sutures. In spite of these numerous differences, it seems impossible to divide the group into two or three major groups. It seems probable, on the other hand, that the group might best be expressed as a single, large, pectinate branch, Chart 1. Therefore, the Strophandria are considered as comprising a single superfamily, the Tenthredinoidea.

The Orthandria present a different condition, Chart 1. They are composed of three distinct groups which may be easily set apart on the basis of head capsule and mesosternum. The Xyelidae and Pamphiliidae are at once segregated from the other Orthandria on the basis of the large presternal bridge, fig. 129 (psb), formed by the fusion of the mesoepisterna anterior to the mesosternum. The two families themselves are remarkably different in respect to the head and mouthparts, but are just as remarkably similar in thoracic structure, legs, and the basic plan

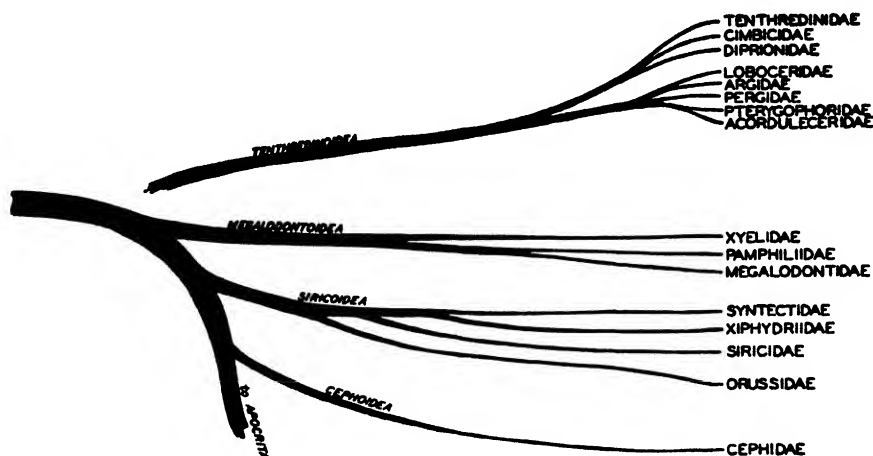


CHART 1.—GENEALOGICAL ARRANGEMENT OF SAWFLY FAMILIES

of the wings. They are therefore considered collectively as the superfamily Megalodontoidea.

The remaining families of the Orthandria are divided into two superfamilies on the basis of the head capsule: (1) the Cephoidea (including Cephidae only) have the occipital foramen separated from the maxacava by a maxapont, fig. 8, and (2) the Siricoidea (including Syntectidae, Xiphydriidae, Siricidae, and Orussidae) have the occipital foramen separated from the maxacava by a genapont, fig. 19.

These two superfamilies are closely related. This is shown by the similarity in the wing venation of the Cephidae and the Syntectidae and Xiphydriidae, the loss or reduction in each of one of the apical tibial spurs of the prothoracic legs and the similar ventral tilting of the tentorium. The Cephidae, however, represent an offshoot of the Siricid stem before the others had developed the genapont. The two lines resulting from this branching have become modified in entirely different characters. The

Cephoidea followed the line leading to a petiolate abdomen and a head capsule with a more open maxacava, whereas the Siricoidea followed the line leading to extreme consolidation of the thorax and abdomen, resulting in the loss of all flexibility between the two, and the development of a stronger head with a more enclosed maxacava.

The selection of the characters mentioned above as being indicative of relationships has been fraught with many difficulties. In the first place, so many instances have been discovered of true parallel evolution that it has been problematic to decide when similarities were significant of relationship or merely another case of parallel evolution. These instances will doubtless have been noticed in a perusal of the foregoing discussion of the morphology. There has frequently occurred, also, the combination of very primitive and very specialized characters in the same form, where it has been necessary to decide which ones were the more significant. In order to harmonize these observations it seems advisable to present a hypothetical reconstruction of the origin and development suggested for the different groups segregated in this treatise.

Members of the early sawfly stem had a simple head capsule, fig. 2, distinct sterno-pleural sutures, figs. 129, 134, slender and multi-segmented antennae, fig. 88, and tibiae with two unmodified apical spurs and at least one to four preapical spurs, fig. 110. This is simply an assemblage of the generalized characters found in existing forms of the group.

The Tenthredinoidea branched off before this collective pattern had changed greatly. After their separation from the main stem, these sawflies developed the strophandrous or turned male genitalia. Very likely the mesosternum resolved itself into its present trapezoidal shape at this time also. The group was exclusively a leaf-feeding one and probably evolved its large number of genera and species concurrently with the increasing diversity and evolution of the surrounding flora. It split up into a number of well-marked groups which correspond to the families recognized in this paper.

The earliest families to emerge from the group were the Pergidae, Argidae, Loboceridae, Perreyiidae, and the Pterygophoridae-Acorduleceridae complex. All these have retained the preapical spurs and the sterno-pleural sutures in at least their primitive genera. They have developed many differences of an apparently adaptive nature—the Pergidae have reduced, clavate antennae; the Argidae have antennae still further reduced, the flagellum composed of only a single, thick segment, fig. 97, which is furcate in some of the males, fig. 98; the Perreyiidae and Pterygophoridae have antennae modified in the opposite direction, with a multi-segmented flagellum, serrate in the female and pectinate in the male (similar to figs. 106 and 105, respectively). There is a series of characters of somewhat the same nature in the wings. Media and first

medio-cubital cross-vein may be parallel or divergent, many of the cross-veins may be present or absent, and the anal veins may assume various patterns. These characters appear in random combination throughout the Tenthredinoidea.

The behavior of the sterno-pleural sutures and the preapical spurs in some of these families is indicative of the condition we find in the more specialized Tenthredinoidea. For instance, in the Argidae the sterno-pleural sutures are present in some members, weak in others, and apparently absent in the remainder; and the preapical spurs of the tibiae are present in the genus *Arge* but not in *Atomacera*, *Sterictiphora*, *Sericocera*, and others. Again, the Acorduleceridae and Pterygophoridae are apparently very closely related and evolved from a common parent, but in the former the sterno-pleural sutures are entirely absent and the preapical spurs present, whereas in the latter the preapical spurs are absent and the sterno-pleural sutures are distinctly present.

The more recently differentiated Tenthredinoidea have lost both sterno-pleural sutures and preapical spurs. They comprise three families, the Diprionidae, Cimbicidae, and Tenthredinidae. These have developed peculiar characteristics which set them off from each other distinctly. The Cimbicidae have conspicuous capitate antennae, fig. 100, and also have the abdominal terga angulate on the lateral margin, so that their ventral portions appear to be pleurites. The Diprionidae are characterized by the antennae, which have thirteen or more segments, serrate in the female, fig. 106, and pectinate in the male, fig. 105. The Tenthredinidae have setaceous, fig. 103, rarely clavate, fig. 101, antennae and a peculiar modification of the caudal margin of the mesoscutellum, fig. 124 (pt), known as the post-tergite.

Most of the Tenthredinidae have another interesting difference from the remainder of the Tenthredinoidea. Instead of both apical spurs of the front tibiae being simple and alike, one of them is furcate at the tip, fig. 114. It is interesting to note that this or some variation of it is the condition found throughout the Orthandria. Not all the Tenthredinidae possess this character. *Athalia* has both spurs unmodified, similar in this respect to the other Tenthredinoidea; in the small species of the leaf-mining Phyllotominae and a few Nematinae the apical incision in the modified spur is absent; but in all the other members of the family which I have seen this furcation is pronounced.

Except for lacking the sterno-pleural sutures and the preapical spurs, the Tenthredinidae are probably the most unmodified family in the entire superfamily. Its primitive genera have an almost hypothetical wing venation, antennae unmodified except by reduction in the number of segments, and a distinct prepectus. In addition, the family is represented at the present time by more genera and species than any other sawfly

family. For this reason the family may be truly called the growing bud at the end of the Tenthredinoid branch.

The other main stem of the sawflies (the Orthandria) had meanwhile broken up into numerous groups. Before this fraction occurred, however, the anterior ends of the sterno-pleural sutures had met on the meson and the mesoepisterna had formed a presternal bridge in at least some measure. Apparently, also, one of the apical spurs of the front tibiae had become furcate as in the Tenthredinidae.

The Megalodontoidea were the first group to break off. This occurred before the head had changed from the primitive open type. This group early resolved itself into its component families, the Xyelidae, Pamphiliidae, and Megalodontidae, which have evolved along entirely different paths and clearly indicate their early separation by their fundamental differences, set forth on page 35.

After the digression of the Megalodontoidea, the Orthandria split dichotomously into the Siricoidea and Cephoidea. Both groups are represented in our fauna only by wood-boring or stem-boring species or parasites of wood-boring insects.

The Siricoidea developed the genaponta, fig. 19, almost immediately after their differentiation as a group. They also lost the preapical tibial spurs. There has been a very marked tendency towards a consolidation of the body sclerites in all four families of this superfamily.

Syntectidae is the most primitive family of the Siricoidea. It has distinct sterno-pleural sutures, fig. 130, which are similar in position to those of the Xyelidae and suggest a close relationship of these two families. The mesoepisterna are curiously produced anteriorly and are probably an orthogenetic expression of this relationship. The pronotum, fig. 122, is like the rectangular type found in the Megalodontoidea and Cephoidea, and forms a convenient intermediate between these sawflies and the remainder of the Siricoidea. The Xiphydriidae, fig. 123, have the pronotum much more reduced on the meson, and have developed a secondary suture across the mesonotum between the wings. The Siricidae, fig. 127, have undergone a great consolidation of the sclerites of the thorax and of the metathorax with the abdomen. The praescutum is only faintly discernible, the transverse suture across the mesonotum is present as two lateral diagonal grooves, and the scutellar sutures have the same groove-like appearance. The mesoepisterna and mesosternum have completely fused, leaving only a very faint trace of the sterno-pleural suture; according to this trace and the position of the furca, figs. 137, 138, there is a very narrow presternal bridge. The entire thorax and base of the abdomen form a solid mass, with no flexibility remaining. The antennae, fig. 18, have migrated ventrally on the head and come to lie adjacent to the

pretentorinae; the clypeus is half turned under, and the labrum is almost entirely concealed under it.

The Orussidae, fig. 142, like the Siricidae, have a solid and inflexible thorax and abdomen. The praescutal sutures are present, but do not join on the meson, continuing longitudinally to the secondary suture across the scutum. This suture is as well marked as in the Xiphydriidae. The wing venation, fig. 177, has been greatly reduced by atrophy, and is obviously a derivative of the Xiphydriid type of venation. The antennae, clypeus, and part of the frontal region have migrated on to the ventral aspect of the head, presumably a more advanced expression of the tendency shown in the Siricid head. In the Orussidae, also, the antennae are adjacent to the pretentorinae, both being situated on the ventral aspect of the head.

The three families Xiphydriidae, Siricidae, and Orussidae comprise an interesting complex. In all of them the paraglossae and alaglossa have become decidedly fused, either entirely or in part. They have the secondary transverse suture across the mesoscutum, which is also a conspicuous feature of many of the Apocrita. All three families, also, have the tentorium deflected antero-ventrally, and in the last two mentioned the antennae and other parts of the head have migrated ventrally.

The Orussidae have been placed as a separate suborder by Rohwer and Cushman (1917) and held as such since then by various authors. The parasitic habit of the larva of *Orussus*, the ventral position of the antennae and the closed condition of the end of the abdomen of the male were the chief characters upon which the family was raised to subordinal rank. Considering that both the Xiphydriidae and Siricidae have tree-boring larvae, there is reason to suppose that an offshoot of their branch might produce a parasite whose host was a wood-borer, as is the host of *Orussus* (*Dicerca*, Buprestidae; see Burke, 1917). The reduction of the thoracic legs in the larvae of *Orussus* could easily be purely adaptative to a parasitic life. It seems no more fundamental than the loss of abdominal legs by the Cephidae and other Siricoidea, which have boring larvae. The ventral position of the antennae in *Orussus* is one of the strongest arguments proving its close relationship to the Siricid stem, rather than one for separating it widely from all the sawfly group. It is true that the Orussidae have some extremely distinctive characters, such as the unique type of male genitalia, fig. 169, the form of the praescutal sutures, the atrophy of the supratentorial arms, and the atrophy of many of the wing veins. But on the other hand they are of decided Siricoid stock and actually possess no more distinctive characters than the Siricidae. For this reason it seems a better expression of their relationship to consider them as belonging to the Siricoidea.

The other major group of the ancestral Siricoid stem developed into

the Cephidae. In these, the wing venation, fig. 175, has remained to the present day almost exactly as we find it in the Syntectidae and Xiphydriidae. The hind wings, however, have lost the short row of bristles present at the base of the wing in the Xyelidae and the two latter families, figs. 171, 176. The preapical spurs on the tibiae are still retained; but the single apical spur on the front tibiae is different from any others in the group, figs. 114-119. There are several characters found in this family which apparently represent the beginnings of specializations found in the Apocrita or higher Hymenoptera: the metanotum is very closely united with the mesonotum, and the first abdominal tergite with the metanotum, whereas a marked constriction has developed between the first and second abdominal terga and a rudimentary articulation exists between them; the corpotentorium has a very small corpotendon and the supratenorial arms join the exoskeleton near the margin of the eye; the cenchri are absent; the mesopostnotal apodeme is long, as in fig. 152; and the wings show a decided tendency towards the atrophy of the first radial cross-vein.

The Braconidae (which are accepted as the most primitive family of the Apocrita) apparently arose from a Cephoid ancestor. The chief differences between the Braconids and the sawflies may be summarized as follows:

Symphyta

1. Abdomen not petiolate (except slightly in Cephidae).
2. Postgenae and maxillariae not shelved in around maxacava.
3. Corpotendon absent (except in Cephidae).
4. Mesopostnotal apodeme short (except in Cephidae, Siricidae).
5. Male genitalia with harpes distinct (except in Cephidae).
6. Cross-vein $1r$ present (except in Orussidae and some Cephidae).

Braconidae

1. Abdomen petiolate, a distinct articulation between tergites 1 and 2.
2. Postgenae and maxillariae angled in to form a shelf around maxacava.
3. Corpotendon distinct and large.
4. Mesopostnotal apodeme long, similar to Cephidae.
5. Male genitalia with harpes entirely fused with gonostipes.
6. Cross-vein $1r$ absent.

This tabulation shows the close relationship of the Cephidae and Braconidae. It is not intended to use this as an argument for grouping the Cephidae with the Apocrita, for they are essentially sawflies in every sense of the word. The significant point is that many specializations of the lower Apocrita beyond the sawflies have at least some expression in the Cephidae. In other words, it establishes the hypothesis that the Cephidae represent the ancestral form of the primitive Apocrita.

The more specialized Apocrita have developed the transverse suture across the mesonotum and the longitudinal condition or entire atrophy of the parapsidal (praescutal) sutures, such as we find in the Orussidae and Siricidae, respectively. These conditions, however, are not found in

the Braconidae, which have a mesonotum similar to that of the Cephidae.

According to the hypotheses set forth in this reconstruction, the Orthandria constitute a veritable experimental ground from a biological sense. The most primitive members are external leaf feeders, the more specialized ones are stem and wood borers, and two separate branches have each produced a parasitic form, the Orussidae from the Siricoidea and the Braconidae from the Cephioidea. The former was accompanied by several changes in the adult insect, but none of these were more than would be expected from an aberrant offshoot. In the case of the Braconidae, however, the entire adult has undergone a radical reorganization which has been a marked change from the prevailing condition among the sawfly groups. This is exemplified in the head, especially the tentorium, and the articulate, petiolate abdomen. The product resulting from this reorganization has apparently been vigorous and well adapted to a predator-parasitoid rôle. Furthermore, this adaptability has been very flexible, as is evidenced by the numerous types of parasitic, predaceous, phytophagous, and omnivorous biologies which have evolved from it. Whereas their closest relatives, the Siricoidea and Cephioidea, are at the present time in the class of decadent groups, the Apocrita constitute a very abundant, virile stem successfully following a large number of avenues of existence.

It is interesting to note in this connection that of all the sawflies the superfamily Tenthredinoidea alone has the appearance of being an ascending and not a decadent group. Among these, the family Tenthredinidae stands out as the most virile stem of the entire superfamily. At the present day it contains approximately eighty per cent of all the species of the Symphyta.

No attempt has been made to place the family Blasticotomidae in the present phylogenetic arrangement. It has been impossible to obtain specimens for dissection of *Blasticotoma filiceti* (Klug), the sole representative of the family. Consequently the course of the sterno-pleural sutures (which are atrophied) and the orientation and composition of the male genitalia could not be determined. Without knowledge of these parts and others which must be dissected out, it is impossible to make any accurate placement of the family.

Comparison with Other Classifications

In the main features of arrangement, the present classification is similar to that of Konow (1905), which was the first really comprehensive one to be outlined. The categories are quite different from Konow's, but this is chiefly due to the subsequent elevation of lower groups to family ranking.

Ashmead (1898) proposed a radically different classification using units based on such characters as wing venation and relative body proportions. It has been abandoned by all authors since that time, and has been found equally untenable by the present author.

The classification proposed by MacGillivray (1908) is subject to much the same criticism as Ashmead's. The entire group is considered as one superfamily, divided into nine families, and one of these, the Tenthredinidae, into twenty-four subfamilies. The basis for the entire classification is the wing venation. Figuring prominently among the characters are the presence or absence of the radial cross-vein, the condition of the anal cells, the parallel or divergent condition of M and *1m-cu*, and cell R 1&2 being appendiculate or not. These characters are subject to variation between the two indicated extremes, and have been one of the richest grounds for parallel development. The use of this single set of characters has led to the following misconceptions: (1) grouping together unlike families due to parallel evolution of certain features of the wings (e.g., Megalodontidae and Siricidae); and (2) improper stratification of groups. This last is well exemplified by his treatment of the Tenthredinidae. The families Argidae, Cimbicidae, and Diprionidae are in reality units of about the same status as the family Tenthredinidae. The family Tenthredinidae includes the subfamilies Nematinae, Selandriinae, Blennocampinae, and others, which are comparable to subfamilies of the Diprionidae and Cimbicidae, not to the entire families themselves. Yet on the basis of only one set of characters, MacGillivray has listed these groups of different status (Diprionidae, Cimbicidae, Nematinae, Selandriinae) as units of the same category (subfamilies).

In the family Tenthredinidae as herein restricted, the wing venation has proved to be the best basis yet known upon which to make subfamily divisions. In these, many of MacGillivray's subfamilies have proved highly satisfactory, but others again reflect the use of too variable characters.

Rohwer (1911e and subsequent emendations) has followed Konow's classification very closely. He has added to that a large number of new characters and made use of superfamily and family categories to bring out more fully the phylogenetic significance of the groupings. The family units are at great variance with those employed by MacGillivray, but seem to be logical from the standpoint of utility and comparability. They are accepted in this paper with but one or two exceptions.

The chief differences between Rohwer's classification and the one embodied herein are as follows: (1) Rohwer considers the Orussidae to represent a separate suborder, the Idiogastra, whereas it is considered here to be a family allied to the Siricidae, Xiphydriidae, and Syntectidae; (2) the Cephidae are here considered as a separate superfamily,

whereas they are grouped with the Megalodontoidea by Rohwer; (3) the unique genus *Syntexis* is placed in the Cephidae by Rohwer, but here is transferred to the superfamily Siricoidea and placed in a separate family, the Syntectidae.

Enslin (1912-18) used a system differing markedly from any of these, in that the Megalodontoidea and Tenthredinoidea of this paper are grouped by him into a single family. This seems to have been done chiefly on the basis of the tibial spurs. The Cephidae were considered a subfamily of the Siricidae. A more complete analysis of this arrangement will show it to be strikingly similar in one or two important respects to that proposed in this paper, except for a difference in the ranking of the different groups. For instance, the tribes and subfamilies used by Enslin are the subfamilies proposed by Rohwer and myself. Aside from this the close relationship of the Cephidae and Siricoidea is expressed, and also the fact that the Tenthredinoidea are more closely related to the Megalodontoidea than to any other group.

Boulange (1924), in his study of the musculature of the male genitalia, arrives at these same two conclusions. He states, furthermore, that the Siricidae have the most primitive male genitalia of any sawfly, and from this infers that this family is the most primitive of the Symphyta. The highly specialized characters of the family indicate rather that it separated from its progenital stem almost as early as any group.

LARVAL CHARACTERS

The morphological data presented by Yuasa (1923) in his classification of larval sawflies and horntails neither substantiates nor refutes the main hypotheses just presented. In the first place, the larvae have relatively few differentiated areas or parts as compared with the adults. For instance, there are no definite sclerites on the thorax and no structures comparable to the male genitalia bearing a number of characters and parts. In the second place, what parts are evident do not present the wide range of difference the same part does in the adult. This is well shown in the maxillae and labia. In the larvae they differ only in number of segments of the appendages and only slightly in shape. In the adults these same parts assume a great variety of shapes.

The most significant larval characters seem to be the lack of segmented thoracic legs in the Siricoidea and Cephoidea. This, however, may be correlated more with the stem-boring habits of this group than with phylogeny. This same condition is approached by the leaf-mining genera of the distantly related Tenthredinidae. The Siricoidea and Cephoidea are further set off in having reduced or atrophied ocellaræ and reduced mouthparts.

On the whole, it would appear that characters affording distinct grouping of the sawfly group into large segregates either are not present or have not yet been located in the larvae. It may well be that their characters are adaptive to their habits and environment to such an extent as to obscure phylogenetic differences.

One valuable indication the larvae do give, the probable antiquity of some dichotomies in our genealogical tree. These points are of considerable interest in a few cases, which will be discussed in detail.

The Xyelidae and Megalodontidae are closely related, yet differ more in head structure of adult than any other two families of sawflies. The larvae show equal diversity. Those of the Xyelidae have larvapods on all segments of the abdomen and no subanal appendages; those of the Megalodontidae have no larvapods but have well developed subanal appendages. This difference adds much weight to the opinion that the dichotomy of these two families is very old.

Yuasa considers that a combination of the characters of these two families would give a hypothetical ancestral larva for the sawflies, with the following: abdomen with larvapods on all segments, subanal appendages, functional metaspriacles, and little indication of annulations on the segments.

The Tenthredinoidea are unique in having some abdominal segments, at least the first and ninth, sometimes also the seventh and eighth, without larvapods while the remainder possess them. This morphological differentiation on the abdomen is probably a significant character, in view of the distinctness of the group based on adults.

A study of the leaf-mining Tenthredinidae brings out clearly how rapidly larval changes accompany burrowing habits. The subfamily Phyllotominae consists of a genus of free leaf feeders, *Caliroa*, and a number of leaf-mining forms, such as *Phyllotoma*, *Metallus*, and *Fenusa*. These latter genera have the antennae reduced from five segments to four, three, two, or one; the thoracic legs sometimes with trochanters and tibiae fused with femur, in one instance (*Phyllotoma*) with the tarsal claws represented by only fleshy tubercles. This does not reach the state of reduction found in the Siricoidea but shows how soon such a state could be acquired in connection with the burrowing habit.

BIOLOGY

The biology of the sawflies adds some interesting points to their phylogenetic considerations. Alone they do not seem of great importance but taken in conjunction with what has just been discussed they present some corroborative evidence. A brief résumé will first be given of the more diagnostic points in their biology. I have definite information only on nearctic families.

TENTHREDINOIDEA.—Larvae external leaf-feeders with the following exceptions: three genera of the Tenthredinidae (*Lycaotella*, *Euura*, and some *Nematus*) are gall makers; several species of *Nematus* form a leaf curl; all the Tenthredinid tribe Phyllotominae except *Caliroa* are leaf miners; one Tenthredinid genus *Caulocampus* is a petiole miner in maple leaves; another, *Hoplocampa*, mines in fruits of Rosaceae; and several Argidae are leaf miners in their early instars. The pupae of the Argidae, Cimbicidae, and Diprionidae are all enclosed in hard cocoons which can be formed on an open surface. The pupae of the Tenthredinidae are divisible into two groups: (1) the subfamilies Cladiinae and most Nematinae form cocoons similar to the preceding; (2) the pupae of the remainder of the family have either a weak cocoon or none and are dependent for protection on earthen cells or chambers in twigs, rotten wood, etc. The pupae are quiescent.

MEGALODONTOIDEA.—Larvae either free leaf feeders, leaf curlers, or feed in the staminate cones of pine. Pupae formed in a cell in the ground. The few recorded observations known indicate that the pupae are active. Mr. J. M. Langston has written me as follows concerning the pupae of *Megaxyela langstoni*: "One interesting point was that the pupae came to the surface of the soil and there cast the pupal skins. They are able to walk before casting these skins." This active condition is similar to the condition found in the Megaloptera. It undoubtedly represents the most primitive pupal condition in the Hymenoptera.

SIRICOIDEA (except Orussidae) AND CEPHOIDEA.—The larvae of these are exclusively stem borers, the Cephidae in smaller stems such as grasses and raspberries, the Siricoidea in trees. The pupa, which is inactive, is formed in a thin cocoon at the terminus of the mine.

ORUSSIDAE.—This family is parasitic on the larvae of Buprestidae (Coleoptera). The larvae are extremely reduced as far as appendages are concerned compared to other members of the family (Rohwer and Cushman, 1917).

In applying this information to the phylogeny, it is evident that the parasitic Orussidae arose from a wood-boring ancestor. Interesting is the fact that its host is a wood-boring beetle larva.

Since the more primitive Apocrita, or higher Hymenoptera, are predator-parasites and the Cephidae are stem borers, there is no biological reason why the former could not have arisen from the latter.

Host Plants

It was thought at one time that a list of plant families indicating the sawfly groups feeding on them would have a marked significance in determining the primitiveness of the sawflies. When the tabulation was

started it was soon found that the exceptions obscured whatever significance there might be in it.

Two circumstances are worthy of note. The commonest hosts are all very primitive plants and include Polypodiaceae (ferns), Pinaceae (conifers), Graminales (grasses and sedges), Amentifera (willows, alders, hickories, oaks, etc.), and Rosaceae (almost every native genus). There are sawflies which feed on other hosts, but aside from these named few sawflies attack them. Thus only a few species of sawflies feed on such highly specialized families as the Ericaceae, Caprifoliaceae, and Compositae.

A few sawfly groups are very narrowly restricted in host range. The family Diprionidae feeds only on Pinaceae, most of the subfamily Selandriinae (Tenthredinidae) only on Polypodiaceae, and in other groups many genera are confined to a single plant genus. A few groups show a striking range of hosts within a single phylogenetic complex. For instance, in the Nematinae (Tenthredinidae), *Pikonema* feeds only on *Picea* (spruce), *Pachynematus* on grasses and sedges, and *Pristiphora* on a wide variety of plants including *Betula*, *Ribes*, *Sorbus*, and some conifers; yet these three sawfly genera are difficult to separate on external characters.

It is evident, therefore, that host relationships must remain purely corroboratory in making decisions on sawfly phylogeny.

In this regard there is an interesting bit of speculation. The sawfly group has been demonstrated to be an offshoot of an early Panorpid branch (Ross, 1936a). It has been shown by several paleontologists that the diversification and splitting up of the Panorpid complex progressed at a rapid gait during the Permian of the Palæozoic era, so it is possible to assume that the sawfly branch arose at this time also. Granting this, it is necessary to assume that ferns and conifers were their earliest hosts, since none of their other hosts were known to exist at that early period. On the basis of this hypothesis it would seem that the sawflies flourished concurrently with a rapidly evolving flora.

SUMMARY OF PHYLOGENY

Every source of evidence shows that the sawflies form two distinct groups, the Strophandria (Tenthredinoidea) and Orthandria (Megalodontioidea, Siricoidea, and Cephoidea).

The Strophandria are a unique, detached group of early origin and have evolved into a large number of phytophagous groups. No existing members can be classified as strictly archaic.

The Orthandria are of a different nature. The archaic family Xyelidae, with its primitive venation and active pupa, links the Hymenoptera to a Mecopteroid ancestor, while the Cephidae link the sawfly

group to the parasitic and more specialized Hymenoptera. This substantiates still further the hypothesis of Ross (1936a) that the Hymenoptera are a close derivative of the Panorpid complex as shown by the wing venation.

The abundance of fundamental differences in head capsule, tentorium, subdivisions of the mesonotum and mesosternum, and structure of larvae, found within the Orthandria eclipse the differences within the Apocrita or higher Hymenoptera. This indicates (1) that the groups contained in the Orthandria are of great geologic age, and (2) that the Orthandria represent the early experimental grounds of the Hymenoptera.

TAXONOMY

The opinions previously expressed in regard to the morphology and phylogeny have been applied in this section to the arrangement and differentiation of the families, subfamilies, and genera represented by the fauna of nearctic America.

CONSTRUCTION OF KEYS

Many of the characters considered of importance in the phylogeny of the group have proved unsatisfactory in making keys for the recognition of the families. Some are confined to one sex, such as the male genitalia; others, such as the mouthparts, are impossible to see without relaxing the specimen; and still others, such as the structure of the head capsule, can be seen only after clearing and dissecting the specimen. In the key to families, therefore, only characters which are easily seen and interpreted have been used. A key is primarily for use in identification and not necessarily for bringing out phylogenetic relationships, and for this reason all the keys given below have been made with a view to practicability and accurate determination.

The keys in this paper are designated for separating only the groups known to occur in the nearctic region. They are purely artificial, the phylogenetic angles being discussed in the text. This is in the interest of simplicity and has aided greatly in making many keys easy to interpret.

IDENTIFICATION OF SEXES

In many keys to the genera it is necessary to key out the two sexes separately. They can be differentiated thus: In the *female*, the apical sternites are cleft by a variously shaped, scabbard-like sheath, fig. 293. In the *male*, the apical sternites are not divided along the meson, fig. 424.

ORDER HYMENOPTERA

SUBORDER SYMPHYTA

The suborder Symphyta includes those Hymenoptera in which there is neither a narrow constriction nor a ball and socket articulation between the first and second abdominal segments, figs. 139-143.

Treatment of Superfamilies

The characterization of the superfamilies is more a matter of phylogenetic interest than an essential to classification. It is easier to construct an artificial key to the families of the entire sawfly group than to burden

the identifier with keys to the superfamilies. These are described on page 33, and no further keys are given.

KEY TO FAMILIES

1. Antennae inserted on the ventral aspect of the head, fig. 24.....**Orussidae**
Antennae inserted on anterior aspect of head, fig. 1.....2
2. Antennae have 3 segments, figs. 97, 98.....**Argidae**
Antennae composed of more than 3 segments.....3
3. Third antennal segment very long, surmounted by a slender terminal filament composed of 9-25 segments, figs. 86, 87.....**Xyelidae**
Antennae without a slender terminal filament subordinate to an elongated third segment.....4
4. Antennae capitate, figs. 99, 100.....**Cimbicidae**
Antennae not capitate, at most clavate, fig. 101.....5
5. Antennae with six segments, fig. 95; scutellum with anterior margin sinuate, fig. 126.....**Acorduleceridae**
Antennae with more than 6 segments; scutellum with anterior margin V-shaped, figs. 120-124.....6
6. Front tibia with two apical spurs, figs. 113, 114.....10
Front tibia with one apical spur, figs. 116-119.....7
7. Mesoscutum with two diagonal furrows running from the lateral margin of the scutum to the anterior margin of the scutellum, fig. 127, y; praescutum almost obsolete.....**Siricidae**
Mesoscutum without diagonal furrows; praescutum distinctly set off by sutures, figs. 121, 123.....8
8. Pronotum reduced to a narrow collar on the meson, fig. 123..**Xiphydriidae**
Pronotum not greatly reduced on the meson, figs. 121, 122.....9
9. Apical spur of front tibia with inner margin pectinate, fig. 118..**Syntectidae**
Apical spur of front tibia with inner margin simple, fig. 119.....**Cephidae**
10. Antennae composed of 7-12 segments, figs. 101-104.....**Tenthredinidae**
Antennae composed of 13 or more segments, figs. 88, 105.....11
11. Antennae slender and simple, fig. 88.....**Pamphiliidae**
Antennae either serrate, figs. 106, 107, or pectinate, fig. 105.....**Diprionidae**

SUPERFAMILY TENTHREDINOIDEA

FAMILY ARGIDAE

This family is at once recognized by its three-segmented antennae, which are furcate in the males of some genera, fig. 98.

Diagnostic characters.—Antennae three-segmented, fig. 97, furcate in the males of some genera, fig. 98. Posterior margin of mesoscutellum without a post-tergite, anterior margin V-shaped or slightly sinuate. Mesosterno-pleural sutures usually present, fig. 134, but sometimes atrophied. Preapical spurs present in one genus, *Arge*. Both apical spurs of front tibiae simple.

At present it does not seem advisable to attempt to divide the Argidae into subfamilies. They obviously form a closely knit group. Furthermore, the family contains many tropical genera, a greater knowledge of which would undoubtedly alter any conceptions based on the nearctic fauna.

KEY TO GENERA

1. Males.....2
Females.....4
2. Third antennal segment furcate for its entire length, fig. 98.....6
Third antennal segment entire, fig. 97.....3
3. Hind wing with cell R_1 closed at apex as in fig. 218.....*Arge* (pt.)
Hind wing with cell R_1 open at apex as in fig. 214.....*Atomacera* (pt.)
4. Both front and hind wings with cell R_1 closed at apex, fig. 218...*Arge* (pt.)
At least hind wing with cell R_1 open at apex, fig. 214.....5
5. Tarsal claws bent over at nearly a right angle, just below middle, fig. 215,
and with the base forming a wide tooth.....*Atomacera* (pt.)
Tarsal claws not bent much, and only towards apex, the base narrow, not
forming a tooth, figs. 216, 217.....6
6. Head wide and shallow, without a raised crest between antennae,
fig. 212.....*Lyrola*
Head not so wide but deeper, with a raised crest between antennae,
fig. 213.....*Sterictiphora*

Arge Schrank

Cryptus Jurine, 1801, p. 163. Monobasic, genotype.—*Cryptus segmentarius* Panzer.
Name set aside by International Zoological Congress, 1935.

Arge Schrank, 1802, p. 209. Genotype by subsequent designation of Rohwer, 1911b.
—*Tenthredo enodis* Linnaeus.

Hylotoma Latreille, 1802, p. 302. Monobasic, genotype.—*Tenthredo rosae* Linnaeus.
Cryptus Panzer, 1805, Heft 88, pl. 17. Monobasic, genotype.—*Cryptus segmentarius*
Panzer.

Corynia Imhof et Labram, 1836, p. 23. Genotype by subsequent designation of
Rohwer, 1911b.—*Corynia rosarum* Imhof et Labram.

Acanthoptenos Ashmead, 1898, p. 212. Genotype by original designation.—*Acanthop-*
tenos weithii Ashmead = *Arge macleayi* (Leach).

Characteristics.—Hind tibiae with a preapical spur on outer margin.
Both wings with cell R_1 closed at apex, fig. 218. Antennae simple in both
sexes, flagellum in female clavate, in male filiform. Tarsal claws simple,
long and slender.

Contains a considerable number of nearctic species which are badly in
need of revision.

Atomacera Say

Atomacera Say, 1836, p. 212. Monobasic, genotype.—*Atomacera debilis* Say.

Micrange Ashmead, 1898, p. 213. Genotype by original designation.—*Atomacera*
ruficollis Norton. *New synonymy*.

Characteristics.—Tibiae without preapical spurs. Wings with cell R_1
open at apex due to atrophy of apex of vein R_1 . Antennae simple in

both sexes, flagellum subclavate. Tarsal claws, fig. 215, bent over at a sharp angle before middle.

As far as known, restricted to the nearctic region, and contains only three or four species.

Sterictiphora Billberg

Characteristics.—Flagellum clavate in female, lyriform in male, fig. 98. Head with distinct, carinate crest between antennal sockets. Front wings with cell R_1 either open or closed at apex, hind wing with this cell open and vein 2A various.

The members of this genus in the broad sense form a closely knit group, united by the lyriform male antennae, mesal crest on the head, and similar general appearance. There is no doubt, however, that the species known at present can be segregated into distinct phylogenetic units which it seems convenient to keep separate. These differences are to be seen chiefly in the genitalia, but most of the groups have some external characteristic correlated with them. At present these groups, here considered subgenera, have been worked out only for those species occurring north of Mexico. When others are known it will probably be necessary to subdivide some groups further.

KEY TO SUBGENERA

1. Tarsal claws with apical tooth cleft, fig. 217.....**Neoptilia**
Tarsal claws with apical tooth simple, fig. 216.....2
2. Front wings with cell R_1 open at apex, fig. 214.....3
Front wings with cell R_1 closed at apex, fig. 218.....**Ptenos**
3. Hind wing with vein 2A atrophied, resulting in the loss of the anal cell, fig. 225.....**Leston**
Hind wing with vein 2A present, anal cell present, fig. 224.....4
4. Hind wing with anal cell much longer than its apical petiole, fig. 223.....**Sterictiphora**
Hind wing with anal cell subequal to or shorter than its apical petiole, fig. 224.....**Sphacophilus**

Subgenus *Ptenos* Norton*

Ptenos Norton, 1872, p. 77. Genotype by subsequent designation of Rohwer, 1911b.
—*Ptenos niger* Norton.

Characteristics.—Front wings with cell R_1 closed at apex, fig. 218, hind wings with vein 2A atrophied, fig. 225. Tarsal claws simple, long and curved at apex, fig. 216. Hind basitarsus shorter than the three following combined.

This subgenus contains probably a dozen nearctic species, known to occur in either Mexico or the extreme southwestern United States.

*Preoccupied. Use *Ptenillus* Malaise, 1937, Entomologisk Tidskrift, p. 56. Genotype by original designation.—*Ptenos nigripictus* Norton.

Subgenus *Neoptilia* Ashmead

Neoptilia Ashmead, 1898, p. 213. Genotype by original designation.—*Neoptilia mexicana* Ashmead.

Characteristics.—Differs from *Ptenos* chiefly in having the tarsal claws cleft at the apex, the two rays close together, fig. 217.

A single species, *N. malvacearum* Cockerell, has been described from North America.

Subgenus *Sterictiphora* Billberg

Sterictiphora Billberg, 1820, p. 99. Monobasic, genotype.—*Hylotoma furcata* Fabricius.

Schizocera Lepeletier, 1828, p. 572. Genotype by subsequent designation of Westwood, 1840.—*Hylotoma furcata* Villers.

Cyphona Dahlbom, 1835, p. 8. Genotype by subsequent designation of Rohwer, 1911b.—*Hylotoma furcata* Villers.

Characteristics.—Differs from *Ptenos* in venation, as follows: front wing with cell R_1 open at apex, hind wing with vein 2A distinct, joining 1A near *cu-a*, so that cell 1A has only a very short petiole, fig. 223.

Contains two nearctic species, *sericea* (Norton) and *prunivora* (Dyar).

Subgenus *Sphacophilus* Provancher

Sphacophilus Provancher, 1889, p. 427. Monobasic, genotype.—*Sphacophilus crawii* Provancher.

Characteristics.—Differs from *Sterictiphora s. st.* chiefly in having cell 1A of the hind wing short, with an apical petiole as long as the cell, fig. 224.

Contains an undetermined number of nearctic species, including many whose range extends into the neotropical region. The South American group, *Brachyphatnus*, Konow (1906, p. 250) is a close relative of this subgenus.

Subgenus *Leston* new subgenus

Characteristics.—As for *Sterictiphora*, having high, sharp median crest between antennae, flagellum clavate in female and lyriform in male, both wings with cell R_1 open at apex, and tarsal claws slender, curved at apex. Differs in having 2A atrophied in the hind wing so that cell 1A is open posteriorly, fig. 225.

Genotype.—*Schizocerus zabriskei* Webster and Malley by present designation.

Contains only a single species, the genotype.

Sterictiphora zabriskei (W. & M.)

Schizocerus zabriskei Webster and Malley, 1900, p. 51.

Schizocerus sericeiformis Rohwer, 1908, p. 112. *New synonymy*.

Schizocerus lineatus Rohwer, 1909, p. 12. *New synonymy*.

Schizocerus collaris Rohwer, 1909, p. 13. *New synonymy.*

Schizocerus johnsoni MacGillivray, 1909b, p. 403. *New synonymy.*

Lyrola new genus

Characteristics.—Head wide and transverse, the area between the antennal sockets almost flat, not produced into a crest, fig. 212. Third antennal segment of female distinctly fusiform and shorter than width of head. Front wing with appendiculate cell absent as in fig. 214. Hind wing with 2A joined to 1A half the distance from base to *cu-a*. Tarsal claws slender, curved towards apex, fig. 216. Hind coxae of males contiguous at apex, of females slightly separated. Male subgenital plate convex and curved dorsad, so that its axis is oblique.

Genotype.—*Schizocera brunniventris* Cresson, original designation.

The neotropical genus *Sericocera* will key out with this one. *Sericocera* differs in having the hind coxae of the female separated by at least their width at apex and the subgenital plate of the male concave transversely, not curved dorsad, its axis therefore longitudinal.

The genotype is the only species known to belong in this new genus.

Lyrola brunniventris (Cresson) new combination

Schizocera brunniventris Cresson, 1880, p. 2, ♂, ♀.

Schizocera tristis Cresson, 1880, p. 52, ♂, ♀. *New synonymy.*

Schizocerus tristis var. *fumipennis* Dyar, 1893, p. 195, ♂, ♀. *New synonymy.*

This species occurs in southern California and Arizona, and has been reared from various legumes, including *Lotus* and *Hosackia*. The abdomen in both sexes varies from rufous through brown to black.

Themos Norton

Themos Norton, 1867, p. 58. Monobasic, genotype.—*Themos hyaline* Norton.

This genus originally included a single species represented by a unique specimen and has not since been studied. The characters used to differentiate it from other Argids are not satisfactory; furthermore, Norton expresses the belief that the locality label "Pennsylvania" of the type specimen is probably an error and perhaps should be Mexico or South America. For these reasons *Themos* is simply mentioned here.

FAMILY ACORDULECERIDAE new family

Diagnostic characters.—Antennae filiform, 6-segmented, fig. 95. Mesoscutellum without a post-tergite, its anterior margin sinuate, fig. 126; praescutal sutures with their posterior portion atrophied, so that postero-mesally the praescutum is confluent with scutum. Meso-

sterno-pleural sutures absent. Middle and hind tibiae with preapical spurs, the apical spurs of the front tibiae simple.

This family contains only one genus, *Acordulecera* Say. It has previously been considered as a subfamily of the Pterygophoridae by Rohwer (1911e). The two differ as follows:

<i>Acorduleceridae</i>	<i>Pterygophoridae</i>
Antennae6-segmented, filiform.	Multisegmented, serrate in ♀, pectinate in ♂ (as in figs. 106, 105, respectively).
TibiaePreapical spurs present.	Preapical spurs absent.
Mesosternum.....Sterno-pleural sutures absent.	Sterno-pleural sutures present.
MesonotumPraescutal sutures atrophied posteriorly.	Praescutal sutures complete.
Anterior margin of scutellum sinuate.	Anterior margin of scutellum V-shaped.
Distribution.....American.	Australian.

The male genitalia of the two families are practically identical, fig. 164, so that there seems little doubt of their close relationship. In view of the striking differences between them, however, it seems advisable to separate the two groups as distinct families.

Acordulecera Say

Acordulecera Say, 1836, p. 210. Monobasic, genotype.—*Acordulecera dorsalis* Say.

The only genus in the family, therefore characterized as in the latter.

The genus is restricted to the nearctic and neotropical regions. Dr. O. Conde, of Riga, Latvia, has revised in manuscript the nearctic species, of which about 20 have been described.

FAMILY DIPRIONIDAE

Diagnostic characters.—Antennae composed of 13 or more segments, serrate in the female, fig. 107, and pectinate, fig. 105, or bipectinate in the male. Mesosterno-pleural sutures atrophied, mesoscutellum with anterior margin V-shaped, posterior margin with an extremely narrow and cord-like post-tergite. Tibiae without preapical spurs; apical spurs of front tibiae simple.

This family has been divided into two subfamilies on the basis of the anastomosis or separation of veins 2A & 3A and 1A in the front wing, and the unipectinate or bipectinate male flagellum. On the basis of other characters, especially genitalia, the family seems too closely knit to necessitate such a grouping.

The best digest of the nearctic members of the group is given by Rohwer, 1918b.

KEY TO GENERA

1. Males.....6
Females.....2
2. Supraclypeal area of head raised into a large tubercle below antennal sockets, fig. 231.....**Monoctenus**
Supraclypeal area not tuberculate, in profile confluent with the clypeus, fig. 232.....3
3. Head and thorax polished, practically impunctate, and metallic blue-black. Antennae with 14 segments.....**Augomonoctenus**
Head and mesoscutellum either not metallic or with dense conspicuous punctuation. Antennae with 16 or more segments.....4
4. Pulvillar pad of hind basitarsus almost as long as the basitarsus, fig. 229. Abdomen greenish-yellow or transversely banded with black or brown and yellow.....**Zadiprion**
Pulvillar pad of hind basitarsus about one-half as long as the basitarsus, fig. 228. Abdomen brown, rufous or darker without transverse bands of yellow.....5
5. Mesoscutellum large, with its anterior margin forming a wide V, and entirely covered with large punctures, fig. 220.....**Diprion**
Mesoscutellum smaller, with its anterior margin forming a narrower V, and only the apical or lateral portions bearing large punctures, fig. 219.....**Neodiprion**
6. Flagellum with all segments unipectinate, fig. 233.....7
Flagellum with at least basal ten segments bipectinate, fig. 234.....8
7. Supraclypeal area of head tuberculate and raised above level of clypeus, fig. 231.....**Monoctenus**
Supraclypeal area not tuberculate, confluent with profile of clypeus, fig. 232.....**Augomonoctenus**
8. Apical five segments of flagellum unipectinate, fig. 235.....**Zadiprion**
All but last segment of flagellum bipectinate, fig. 236.....9
9. Mesoscutellum large, with its anterior margin forming a wide V, and entirely covered with dense, coarse punctuation, fig. 220.....**Diprion**
Mesoscutellum smaller, with its anterior margin forming a narrower V, and with much sparser punctuation, fig. 219.....**Neodiprion**

Monoctenus Hartig

Lophyrus subg. *Monoctenus* Hartig, 1837, p. 171. Monobasic, genotype.—*Tenthredo juniperi* Linnaeus.

Characteristics.—Front wings with Sc_2 present, 2A & 3A fused for a variable distance with 1A. Head with supraclypeal area tuberculate, fig. 231. Antennae serrate in female, unipectinate in male, with 14-22 segments. Head and thorax not metallic.

Five nearctic species have been described.

Augomonoctenus Rohwer

Augomonoctenus Rohwer, 1918b, p. 81. Monobasic, genotype.—*Augomonoctenus libocedrii* Rohwer.

Characteristics.—Front wings with Sc_2 absent, 2A & 3A fused for a distance with 1A. Head with supraclypeal area confluent in profile with clypeus, area behind and above eyes considerably swollen and enlarged. Antennae of female serrate, 14-segmented, of male unipectinate. Head and thorax metallic blue-black with practically no punctuation.

Contains only one species, the genotype.

Zadiprion Rohwer

Neodiprion subg. *Zadiprion* Rohwer, 1918b, p. 83. Genotype by original designation.—*Diprion grandis* Rohwer.

Characteristics.—Front wings with at least base of Sc_2 present, and 2A & 3A separated from 1A by a cross-vein. Head with supraclypeal area not tuberculate, area above and behind eyes wide and flattened. Antennae of female serrate, with 20-26 segments, male with 22-26 segments, the flagellum bipectinate except for the terminal five segments which are moniliform and undivided, fig. 235. Female with pulvillar pad of hind basitarsis subequal to length of basitarsus, fig. 229, male with pad only one-fourth length of basitarsus.

The genus contains four species.

Neodiprion Rohwer

Neodiprion Rohwer, 1918b, p. 83. Genotype by original designation.—*Lophyrus lecontei* Fitch.

Characteristics.—Differs from *Zadiprion* in the following points: male flagellum with all segments bipectinate except the apical one, fig. 236; female with pulvillar pad of hind basitarsus one-half or less length of basitarsus, fig. 228.

Contains a large number of nearctic species which have not been revised since 1869.

Diprion Schrank

Pteronus Jurine, 1801, p. 163. Monobasic, genotype.—*Tenthredo pini* Linnaeus. Name set aside by International Zoological Congress, 1935.

Diprion Schrank, 1802, p. 209. Genotype by subsequent designation of Rohwer, 1910d.—*Tenthredo pini* Linnaeus.

Lophyrus Latreille, 1802, p. 302. Monobasic, genotype.—*Tenthredo pini* Linnaeus. Preoccupied.

Anachoreta Gistel, 1848, p. 9. New name for *Lophyrus* Latreille.

Cristiger Gistel, 1848, p. 144. Monobasic, genotype.—*Tenthredo pini* Linnaeus.

Characteristics.—Similar to *Neodiprion*, with the following principal exception: scutellum large, its lateral margins fairly long, anterior margin forming a wide V, and densely covered with large punctures, fig. 220.

The genus is Eurasian in the native sense, but a few species have become established in recent years on conifers in North America.

FAMILY CIMBICIDAE

Diagnostic characters.—Antennae capitate, fig. 100. Lateral margins of the abdomen sharply angulate. Mesosterno-pleural sutures barely indicated by a slight ridge; mesoscutellum without a post-tergite and with the anterior margin V-shaped; tibiae without preapical spurs, and apical spurs of the front tibiae simple.

This family has been divided into two subfamilies on the basis of the anastomosis or separation of 2A & 3A and 1A, but the division seems to serve no useful purpose, so it is not used here.

KEY TO GENERA

1. Posterior coxae contiguous at base, fig. 227.....*Zaraea*
Posterior coxae well separated at base, fig. 226.....2
2. Posterior femora with a ventral tooth near apex, fig. 230.....*Trichiosoma*
Posterior femora without a ventral tooth.....*Cimbex*

Zaraea Leach

Zaraea Leach, 1817, p. 113, no. 4. Monobasic, genotype.—*Tenthredo fasciata* Linnaeus.

Abia Leach, 1817, p. 113, no. 5. Genotype by subsequent designation of Curtis, 1825.—*Tenthredo sericeus* Linnaeus.

Parabia Semenov, 1891, p. 174. Genotype by original designation.—*Parabia jakowlewi* Semenov.

Characteristics.—Posterior coxae contiguous at base, fig. 227, front wings with 2A & 3A fused for a distance with 1A. Hind femora unarmed. Antennal club, fig. 99, not sharply set off from remainder of antennae.

Five species have been assigned to this genus in the nearctic region.

Trichiosoma Leach

Trichiosoma Leach, 1817, p. 108. Genotype by subsequent designation of Curtis, 1825.—*Tenthredo lucorum* Linnaeus.

Characteristics.—Body conspicuously hairy. Posterior coxae well separated at base. Posterior femora with a ventral tooth near apex, the tooth much larger in male than in female. Front wings with 1A and 2A & 3A separated by a short cross-vein. Antennal club much more sharply set off from the remainder of the antenna. Mandibles almost perfectly symmetrical, much longer and sharper in the male than the female, figs. 221, 222.

The several described nearctic species are badly in need of intensive study to determine the species limits.

Cimbex Olivier

Crabro Geoffroy, 1762, p. 261. Genotype by subsequent designation of Bradley, 1919.

—*Crabro humeralis* Fourcroy. Name set aside by International Zoological Congress, 1935.

Clavellarius Olivier, 1789, p. 22. Genotype by subsequent designation of Latreille, 1810.—*Tenthredo lutea* L. Application has been made to the International Commission on Zoological Nomenclature to have this name set aside, as with *Crabro*.

Cimbex Olivier, 1790, p. 762. New name for *Clavellarius* Olivier.

Clavellaria Lamarck, 1801, p. 264. Emendation of *Clavellarius* Olivier.

Characteristics.—Differs from *Trichiosoma* as follows: Body not hairy. Hind femora unarmed beneath. Mandibles asymmetrical, dextral one polished, with a long, thin, apical tooth, sinistral one striate and roughened, apical tooth blunt and short.

The taxonomic status of the nearctic species of this genus is similar to the above.

FAMILY TENTHREDINIDAE

Diagnostic characters.—Antennae with 7-10 segments, varying in shape from setaceous and filiform, fig. 93, to clavate, figs. 101-103, the male of *Cladius pectinicornis* (Geof.) having the first three or four segments of the flagellum pectinate, fig. 104. Mesothorax with sterno-pleural sutures lacking, anterior margin of scutellum V-shaped and the posterior margin usually with a distinct post-tergite, figs. 124-125. Tibiae without preapical spurs; apical spurs of front tibiae (except in some Nematinae) with the longer spur cleft at the apex, fig. 114.

The division of this family into units has been one of the most controversial subjects in the study of sawflies. In the last thirty-five years different arrangements have been proposed by Ashmead (1898), Konow (1905), MacGillivray (1906), Rohwer (1911e), and Enslin (1912). The opinions brought out by these authors are startling in their great divergence. In attempting to arrive at the correct groupings of the genera contained in the family it soon became evident that there were no characters known at present which would separate the family by simple divisions into clean-cut subfamilies. For this reason it was necessary to adopt a different line of attack, which is embodied in the following procedure:

1. An exhaustive survey was made of all the genera, and their characters were tabulated.

2. The genera resembling each other more than any other genus were grouped into units. These were homogeneous by the very nature of their selection. This step sorted out about three-quarters of the genera.

3. The remaining genera were then studied in comparison with the groups formed in step 2. Many resembled one or another group so closely that they were placed in it. Others proved to be connecting forms between two groups which had perforce to be united into one. After this there remained less than half a dozen genera which had not been satisfactorily placed.

4. By a comparison of these genera and generic units with each other and with other groups of sawflies, a hypothetical type or primitive ancestor was deduced. From this hypothetical ancestor all the conditions present in the Tenthredinoidea could be derived through comparatively simple changes.

5. After the deduction of the primitive ancestor, the generic units and the unplaced genera were arranged in a family tree in such a way that there was as far as possible a progression of all characters from the generalized or hypothetical to the specialized. This involved considerable "trial and error" manipulation.

Principal Sets of Characters Used

Cervical sclerites.—In the more primitive members of all the subfamilies the cervical sclerites are angulate and separated on the meson, fig. 155. In the Allantinae and Tenthredininae the more specialized genera have the mesal margins truncate and adjacent, figs. 157, 158, as is the case with the Dolerinae. In all three subfamilies this condition is probably for the purpose of strengthening the head articulation, and has been evolved independently in each group.

Mandibles.—A first glance at the mandibles of different members of the family gives the impression of random diversity (Plate III). The more different types are the four-toothed mandibles of the specialized Tenthredininae, figs. 42, 43, the scythe-like right mandibles of the specialized Allantinae, the curious bidentate type shown in fig. 47, and the flattened knife-like mandibles of the specialized Nematinae, fig. 59. Yet almost all of these different types may be traced back through the more primitive members of the subfamily to a simple bidentate type, figs. 46, 51, 53, and 57. The ancestor of the family undoubtedly possessed these simple mandibles, and each group branching away from it has ultimately developed its own characteristic modifications of these appendages. Various types of mandibles within the family are shown on Plate III arranged genealogically.

Anal veins.—An interesting case of reaching the same modification from the same basis by different methods is shown in the condition of the anal veins. The unmodified anal region of the front wing of the Tenthredinidae is the same as that in the sawfly ancestor, having the anal cross-vein present and 2A & 3A forming a distinct angle where they join, fig. 203. In the Nematinae, figs. 202, 200, 198, 2A has gradually fused first with the anal cross-vein then basally along 1A, reducing the first anal cell to a small loop. Finally the distal portion of this loop has atrophied, leaving only the basal portion of 3A present as a short stub. In the Blennocampinae the same fusion of 2A & 3A with the anal cross-

of groups which have arisen from the parent stock in a radiating, palmate fashion, Chart 2; (2) in many cases the primitive genera of some branches are more difficult to separate from the primitive genus of another branch than from specialized genera of the same branch.

It seems apparent that the hypothetical ancestor of the family possessed (1) a prepectus; (2) bidentate mandibles; (3) simple antennae; (4) proximal anal cell contracted in middle and separated from the distal anal cell by the anal cross-vein, as in fig. 203; (5) media in front wing joining radius at point of separation of R_s , and probably fluctuating in respect to being parallel or not to $2m-cu$.

This condition is found only in some specimens of the genus *Hemitaxonus*, but is approached by most genera in its subfamily, the Selandriinae. We may, then, safely consider the Selandriinae to be the most primitive subfamily of the Tenthredinidae.

From some such condition there has been a steady evolution along several diverse lines, leading ultimately to such specialized forms as the higher Nematinae, Tenthredininae, and Allantinae.

KEY TO SUBFAMILIES

1. Front wings with vein 2A & 3A complete and not fused with 1A, figs. 183, 185, 203.....2
 Front wings with vein 2A & 3A either partially atrophied, figs. 205, 209, or fused for a distance with 1A, fig. 201.....9
2. Front wings with anal cross-vein present, fig. 181.....3
 Front wings with anal cross-vein absent, fig. 183.....Selandriinae, pt.
3. Front wings with $2r-m$ present, fig. 181.....4
 Front wings with $2r-m$ absent, fig. 182.....Dolerinae
4. Front wings with proximal anal cell markedly constricted near base, figs. 203, 204, vein M at most joining R very little proximad of fork of R_s , fig. 184.....5
 Front wings with proximal anal cell only feebly constricted, fig. 197, vein M joining R half its length proximad of fork of R_s , fig. 196.....Tenthredininae
5. Mesopleurae rugose with large, crater-like punctures, fig. 329.....Allantinae, pt.
 Mesopleurae at most with separate, inconspicuous punctures.....6
6. Front wings with $R_s + M$ straight, fig. 186.....7
 Front wings with $R_s + M$ markedly curved, fig. 184.....8
7. Front wings with M parallel with $1m-cu$, fig. 186.....Allantinae, pt.
 Front wings with M and $1m-cu$ divergent, fig. 185.....Phyllotominae, pt.
8. Front wings with proximal anal cell as long as distal anal cell, fig. 204.....Adelestinae
 Front wings with proximal anal cell twice as long as distal anal cell, fig. 181.....Selandriinae, pt.
9. Front wing with M partially atrophied, fig. 195.....Nematinae, pt.
 Front wing with M present for its entire length, fig. 193.....10
10. Front wings with M and $1m-cu$ parallel or nearly so, figs. 192, 194.....11
 Front wings with M and $1m-cu$ markedly divergent, figs. 187, 191.....13

11. Front wings with M joined to R half-length of M proximad of fork of R_s , fig. 194.....**Tenthredininae**, pt.
Front wings with M joined to R at or near fork of R_s , fig. 192.....12
12. Front wings with proximal abscissa of 2A & 3A distinct for its entire length, fused to 1A for only a short distance, fig. 192.....**Lycotinae**
Front wings with proximal abscissa of 2A & 3A atrophied for a distance, figs. 190, 208.....**Blennocampinae**, pt.
13. Front wings with M joined to R half-length of M proximad of fork of R_s , fig. 191, giving cell 1M five sides.....**Nematinae**, pt.
Front wings with M joined to R at or near fork of R_s , fig. 188, cell 1M not markedly five-sided.....14
14. Front wings with 2r absent.....**Cladiinae**
Front wings with 2r present, but sometimes faint.....15
15. Prepectus present, fig. 243.....**Blennocampinae**, pt.
Prepectus absent.....**Phyllotominae**, pt.

SUBFAMILY SELANDRIINAE

Prepectal suture present as a distinct suture or a furrow. Propleurae, fig. 155, with mesal margins pointed and not meeting. Front wings, fig. 181, with M either parallel with *lm-cu* or not, meeting R at or near fork of R_s ; $R_s + M$ with a decided bend; these conditions obscured in *Selandria* due to the enlargement of R, fig. 183. Anal cross-vein present or absent; when present the proximal anal cell is considerably longer than the distal cell. Mesopost-tergite normal.

The members of this subfamily are quite uniform in fundamental structure. The chief differences occur in the proportions of the antennae, tarsal claws, shape of clypeus and male genitalia. The range of variation in genitalia within the genus *Strongylogaster*, however, is almost as great as the known extremes in the subfamily, so that their study concerns species more than genera.

In addition to having an abundant nearctic fauna, the Selandriinae have developed greatly in the neotropical regions. Several species taken in Arizona and New Mexico represent this neotropical assemblage in the United States.

KEY TO GENERA

1. Front wing with anal cross-vein present, fig. 181.....2
Front wing with anal cross-vein absent, fig. 183.....4
2. Prepectus a distinct sclerite, separated from episternum by a suture, fig. 243.....3
Prepectus a raised shoulder, separated from episternum by a furrow, fig. 244.....**Strongylogaster**
3. Antennae with sixth segment more than twice as long as wide, fig. 238.....**Hemitaxonus**
Antennae with sixth segment less than twice as long as wide, fig. 237.....**Eriocampidea**

4. Mesepisternum with an inverted V-shaped prepectal suture, forming a prepectus-like area on the postero-dorsal corner of the sclerite, in addition to the true prepectus on the anterior angle, fig. 242. **Selandria**
Mesepisternum without this posterior "prepectus," only the anterior prepectus present, fig. 243. 5
5. Antennae with last four segments reduced in size, together less than twice the length of third segment; flagellum at least somewhat fusiform; pedicel longer than wide, fig. 241. **Aneugmenus**
Antennae with total length of last four segments three or four times as long as third segment; flagellum almost filiform; pedicel no longer than wide, fig. 240. 6
6. Prepectus and adjoining portion of episternum flat, on the same plane, and separated by a line-like suture, fig. 243. **Eustromboceros**
Prepectus shoulder-like, raised above level of episternum, and separated from it by a depressed suture or furrow, fig. 244. **Strongylogaster**

Hemitaxonus Ashmead

Hemitaxonus Ashmead, 1898, p. 311. Genotype by original designation.—*Taxonus dubitatus* Norton.

Epitaxonus MacGillivray, 1908b, p. 365. Genotype by original designation.—*Taxonus albidopictus* Norton.

Characteristics.—Clypeus truncate or slightly emarginate; antennae long and slender, fig. 238; body long and slender. Some specimens with M and 1m-cu of front wing distinctly diverging. Contains three or four species.

Eriocampidea Ashmead

Eriocampidea Ashmead, 1898, p. 256. Genotype by original designation.—*Eriocampidea arizonensis* Ashmead.

Cockerellonis MacGillivray, 1908b, p. 365. Genotype by original designation.—*Cockerellonis occidentalis* MacGillivray = *Eriocampidea arizonensis* Ashmead.

Characteristics.—Clypeus slightly emarginate; antennae short, fig. 237; body of medium robustness.

Represented by a single southwestern species, *E. arizonensis*.

Aneugmenus Hartig

Characteristics.—Anal cross-vein absent in front wing. Antennae with pedicel longer than wide, flagellum fusiform and proportioned as in fig. 241. Tarsal claws with an inner tooth which is parallel to outer and quite stout, fig. 245. Prepectal suture varying from a line to a deep furrow.

The larger species of this group (occurring in the tropics) have been considered as members of *Stromboceros* Konow, but they differ radically from that genus in antennae and tarsal claws and instead are related to the smaller northern species usually considered as decidedly not congeneric.

KEY TO SUBGENERA

1. Legs entirely lemon yellow.....**Aneugmenus**
 Legs mostly black.....**Stromboceridea**

Subgenus *Aneugmenus* Hartig

Aneugmenus Hartig, 1837, p. 253. Monobasic, genotype.—*Tenthredo* (*Emphytus*) *coronata* Klug.

Polyselandria MacGillivray, 1914a, p. 104. Genotype by original designation.—*Selandria floridana* MacGillivray = *Aneugmenus flavipes* var. *flavitaris* Rohwer.

Contains three or four species set off by their short antennae, with the third segment slightly longer than half the length of the last four segments together.

Subgenus *Stromboceridea* Rohwer new combination

Stromboceros subgenus *Stromboceridea* Rohwer, 1911d, p. 392. Genotype by original designation.—*Stromboceros* (*Stromboceridea*) *pilosulus* Rohwer.

Contains many Mexican species, set off by the short terminal segments of the antenna, the last four being little longer than the third. A few species have been taken in the extreme southwestern United States.

Selandria Leach

Selandria Leach, 1817, p. 126. Genotype by subsequent designation of Brullé, 1846.—*Tenthredo serva* Fabricius.

Coryna Lepeletier, 1828, p. 567. Genotype by subsequent designation of Rohwer, 1911b.—*Selandria flavans* Klug.

Paraselandria Ashmead, 1898, p. 255. Genotype by original designation.—*Selandria flavescens* Thomson = *Selandria flavans* Klug.

Selandridea Rohwer, 1911d, p. 388. Genotype by original designation.—*Selandridea vanduzeei* Rohwer.

Pseudoselandria MacGillivray, 1914a, p. 103. Monobasic, genotype.—*Pseudoselandria oxalata* MacGillivray = *Selandria vanduzeei* (Rohwer).

This is an aberrant genus in many respects. In the hind wing 1r-m joins R basad of R₄ and cu-a joins the anal veins at the union of 1A and 2A & 3A. In *S. vanduzeei* (Roh.), the front wing has costa and radius greatly swollen, fig. 183, and this occurs to some extent also in the other nearctic species, *S. decorata* Cress.

Eustromboceros Rohwer new combination

Stromboceros subgenus *Eustromboceros* Rohwer, 1911d, p. 394. Genotype by original designation.—*Stromboceros* (*Eustromboceros*) *melanopterus* Rohwer.

Characteristics.—Front wings without anal cross-vein. Antennae stout, filiform, the segments of the flagellum decreasing only slightly in length from base to apex; pedicel almost twice as broad as long, fig. 240.

Tarsal claws long and slender, with a narrow minute inner tooth midway to base.

A few unidentified specimens from Arizona belong to this genus. They may represent species already described from Mexico.

Strongylogaster Dahlbom

Strongylogaster Dahlbom, 1835, p. 13. Genotype by subsequent designation of MacGillivray, 1908b.—*Tenthredo cingulata* Fabricius.

Thrinax Konow, 1885a, p. 19. Genotype by subsequent designation of MacGillivray, 1908b.—*Strongylogaster contigua* Konow. *New synonymy*.

Prototaxonus Rohwer, 1910a, p. 49. Monobasic, genotype.—*Prototaxonus typicus* Rohwer. *New synonymy*.

Pseudotaxonus A. Costa, 1894, p. 157. Monobasic, genotype.—*Tenthredo filicis* Klug. *New synonymy*.

Polystichophagus Ashmead, 1898, p. 310. Genotype by original designation—*Tenthredo filicis* Klug.

Of the five names listed above, *Pseudotaxonus*, *Polystichophagus*, and *Prototaxonus* are based on species which possess the anal cross-vein, the character upon which they have hitherto been separated from the other members of the genus. *Thrinax* and *Strongylogaster* lack this cross-vein. These latter two differ from each other in the tarsal claws, *Thrinax* having a claw without a tooth and *Strongylogaster* one with a very small tooth. In the absence of other differences this does not seem to be of much generic importance.

In a survey of the species of the nearctic fauna of *Strongylogaster* it is strongly evident that the genus can best be divided into groups on the basis of the male and female genitalia. One group, including *lineata* Christ, *longulus* Norton and *distans* Norton, has the sheath with large, lateral, wing-like expansions; another, including *tacitus* (Say), has a small sheath with small cup-like lateral expansions; and still another, including *politus* Prov., has a small sheath without lateral ornamentation. These groupings are substantiated by the punctuation of head and thorax and by various characters of the clypeus. The species hitherto placed in *Pseudotaxonus* (*filicis* and *tibialis*) agree in sheath, punctuation, and clypeus with the group including *politus* Prov., so closely that the latter group is evidently related more to *Pseudotaxonus* than to many other species of *Strongylogaster* s. st. It will be seen from this that the division previously made on the basis of the inter-anal cross-vein is an unnatural one. When a detailed study of the genus is made, *Pseudotaxonus* and *Thrinax* may serve to designate subgeneric units if these are necessary in the classification.

ADELESTINAE new subfamily

Prepectus absent. Mesonotum with post-tergite apparently not differentiated. Propleurae with mesal margins narrow and pointed, as in

fig. 155. Front wings, fig. 184, with full complement of veins and cross-veins; R + M with a distinct bend; *a* transverse; cell DA almost as long as cell PA. Hind wings with *1r-m* joining R₁ near its separation from R.

This subfamily is erected for a single species originally described by Norton (1867, p. 254) as *Selandria nova*. The species was relegated to the "lost" list. Recently, however, I was fortunate in obtaining for study a female so identified by Harrington, and undoubtedly Norton's species.

The bent vein R + M places the species definitely in the Selandriine group. It differs from the Selandriinae in lacking a prepectus and in the long distal anal cell; from the Dolerinae in possessing cross-vein *2r-m*, and in having the anal cross-vein transverse; and from both in lacking a post-tergite.

Adelesta new genus

Characteristics.—Body short and robust, shining, with practically no punctate areas. Head with antennae slightly serrate, fig. 239, of approximately the same thickness throughout. Clypeus very slightly emarginate. Labrum narrow and triangular. Mandibles not fully visible, but short, stocky, and at least bidentate. Malar space as wide as is middle of front tibiae. Legs with basitarsus subequal to following three together. Tarsal claws long and slender, without an inner tooth.

Genotype.—*Selandria nova* Norton (original designation).

SUBFAMILY DOLERINAE

Characteristics.—Prepectus absent. Mandibles quadridentate or tridentate, fig. 52. Cervical sclerites approximate and semitruncate on meson. Front wings with *2r-m* absent, both anal veins present, separated by an oblique anal cross-vein, and with cell PA constricted near middle, fig. 182. Hind wing with typical venation, possessing *3r-m*, *m-cu* and 2A.

Contains only a single genus, *Dolerus*.

Dolerus Panzer

This genus contains over 40 described nearctic species of which most are in *Dolerus s. st.* and only four in *Loderus*. These have been revised by Ross (1931 and 1935a).

KEY TO SUBGENERA

1. Eyes emarginate mesally, fig. 246, and long.....*Loderus*
- Eyes straight mesally, fig. 247, and short.....*Dolerus*

Subgenus *Dolerus* Panzer

Dolerus Jurine, May 30, 1801, p. 163. *Genotype*.—*Tenthredo gonager* Fabricius.
Set aside by International Zoological Congress, 1935.

Dolerus Panzer, September 3, 1801, Heft 82, pl. 11. Monobasic, genotype.—*Dolerus pedestris* Panzer = *pratensis* (Linnaeus).

Dosytheus Leach, 1817, p. 127. Genotype by subsequent designation of Brullé, 1846.—*Tenthredo eglanteriae* Fabricius = *Dolerus pratensis* (Linnaeus).

Characteristics.—Head and thorax partially or completely rugose or coarsely punctate. Antennae setaceous or slightly fusiform. Tarsal claws with a tooth, either large or small.

Subgenus *Loderus* Konow

Loderus Konow, 1890, p. 240. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo pratorum* Fallén.

Similar to *Dolerus s. st.*, except as mentioned in the key. Some of the species lack an inner tooth on the tarsal claws.

SUBFAMILY PHYLLTOMINAE

Characteristics.—Prepectus absent. Cervical sclerites pointed mesally, not approximate. Mandibles variable, either bidentate or tridentate. Front wings with M and 1*m-cu* divergent; first abscissa of R₁ present or absent, 2*r-m* always present; anal veins extremely variable. Venation of hind wings variable, 3*r-m* always absent.

The genus *Caliroa* is the most generalized member of the group. It possesses bidentate mandibles, front wings with anal veins fully represented, and hind wings with cell R closed, and cross-vein *m-cu* present. The larvae are external, slug-like, leaf feeders.

The remaining members are leaf miners in the larval stage. The mandible pattern changes to a tridentate condition, fig. 55, but other changes are almost entirely due to atrophy of veins. The ultimate reduction is shown in some species of *Fenusa*, in which only 1A is left in either pair of wings, the front wings lack the base of R₁, and the hind wings have cell R open and cross-veins 3*r-m* and *m-cu* both absent.

The few small genera comprising this group have been very poorly understood in North American literature, as can well be seen in the discussion of *Entodecta*, p. 71.

KEY TO GENERA

1. Front wings with vein 2A & 3A well marked for its entire length, figs. 203, 205.....2
 Front wings with 2A & 3A with conspicuous portions of the basal abscissa atrophied, figs. 207, 209.....3
2. Head with anterior aspect markedly convex, fig. 251.....*Caliroa*
 Head with anterior aspect depressed between eyes and meson, fig. 252.....*Phyllotoma*
3. Hind wings with cell R₁ open at apex, fig. 259.....4
 Hind wings with cell R₁ closed at apex, fig. 258.....5

4. Mesopleurae black **Fenusa**
 Mesopleurae yellow or rufous..... **Profenusa**
5. Antennae with third segment nearly as long as the fourth and fifth together,
 segments 4 to 9 diminishing only slightly, fig. 253..... **Scolioneura**
 Antennae more nearly with all segments of flagellum gradually diminishing
 in length, fig. 254..... **6**
6. Front wing with *2r* curving sharply down to meet *R*_s at almost a right
 angle, fig. 250..... **Entodecta**
 Front wing with *2r* curving only gradually and meeting *R*_s obliquely, fig.
 257..... **Metallus**

Caliroa O. Costa

- Caliroa* O. Costa, 1859, p. 59. Monobasic, genotype.—*Caliroa sebetia* O. Costa = *cinxia* (Klug).
Eriocampoides Konow, 1890, p. 239. Genotype by subsequent designation of MacGillivray, 1909a.—*Tenthredo limacina* Retzius = *Caliroa cerasi* (Linnaeus).
Perichistoptera Ashmead, 1898, p. 255. Genotype by original designation.—*Monostegia quercus-alba* Norton.
Endelomyia Ashmead, 1898, p. 259. Genotype by original designation.—*Monostegia rosae* Harris = *Caliroa aethiops* (Fabricius).

Characteristics.—Head robust, fig. 251, anterior aspect convex. Mandible bidentate. Antennae slender and slightly fusiform. Front wings, fig. 185, with first abscissa of *R*_s, and all anal veins present. Hind wings with cross-vein *m-cu* present and 2A present.

Contains about a dozen species which have not been revised thoroughly.

Phyllotoma Fallén

- Phyllotoma* Fallén, 1829, p. 25. Genotype by subsequent designation of Rohwer, 1911b.—*Phyllotoma vagans* Fallén.
Heterarthrus Stephens, 1835, p. 94. Monobasic, genotype.—*Tenthredo* (*Emphytus*) *ochropoda* Klug.
Decatria Stephens, 1835, p. 94. Monobasic, genotype.—*Tenthredo* (*Emphytus*) *ochropoda* Klug.
Druida E. Newman, 1838, p. 484. Monobasic, genotype.—*Druida parviceps* E. Newman = *Phyllotoma nemorata* Fallén.
Phlebatrophia MacGillivray, 1909a, p. 345. Monobasic, genotype.—*Phlebatrophia mathesoni* MacGillivray = *Phyllotoma nemorata* Fallén.

Characteristics.—Head narrowed, with elongate concavities running along the inner margins of the eyes, appearing excavated from dorsal view, fig. 252. Antennae long, slender, and filiform, with 10-12 segments. Venation complete but with many parts faint. Hind wings with *m-cu* absent.

Contains a single species in North America, *P. nemorata* Fallén, which is probably an introduced European species.

Scolioneura Konow

- Scolioneura* Konow, 1890, p. 249. Genotype by subsequent designation of MacGillivray, 1909c.—*Tenthredo* (*Allantus*) *betuleti* Klug.

Parabates MacGillivray, 1909c, p. 262. Genotype by original designation.—*Parabates histrionicus* MacGillivray. *New synonymy*.

Melanobates MacGillivray, 1916, p. 158. Monobasic, genotype.—*Parabates leucostomus* Rohwer. *New synonymy*.

Characteristics.—Head robust. Antennae as in fig. 253, with third segment subequal to fourth and fifth together. Venation variable; front wing with first abscissa of R_s faint or absent and both anal cells open posteriorly; hind wing with cell R_1 closed at apex, fig. 258, and cell 1A also closed.

Contains six described nearctic species which have not yet been revised.

Entodecta Konow

Entodecta Konow, 1886, p. 184. Genotype by subsequent designation of MacGillivray, 1909c.—*Tenthredo* (*Allantus*) *pumila* Klug.

Polybates MacGillivray, 1909c, p. 264. Monobasic, genotype.—*Polybates slossonae* MacGillivray. *New synonymy*.

Differs from *Scolioneura* chiefly in the antennae, which have all the segments of the flagellum gradually diminishing in length.

This genus contains only a single known nearctic species, whose synonymy is given below. The species *alaskana* Kincaid, placed in this genus by MacGillivray, belongs in *Scolioneura*.

The head sculpture and antennal proportions resemble *Metallus* in many respects and it may be necessary later to consider *Entodecta* as a synonym of that genus. This latter view is held by Benson, 1936.

Entodecta capitalis (Norton) new combination

Selandria capitalis Norton, 1867, p. 247, ♀.

Polybates slossonae MacGillivray, 1909c, p. 265, ♀. *New synonymy*.

Polybates secundus Rohwer, 1910c, p. 202, ♀. *New synonymy*.

Entodecta humilis Konow, 1908, p. 84, ♀. *New synonymy*.

This species varies somewhat in color and has a wide distribution, ranging from the Atlantic to the Pacific. The name *capitalis* was referred to *Metallus* by MacGillivray (1909c), but an examination of Norton's type proves it to be a light specimen of the species described by MacGillivray as *Polybates slossonae*.

Metallus Forbes

Metallus Forbes, 1885, p. 87. Monobasic, genotype.—*Metallus rubi* Forbes.

Characteristics.—Front wing without basal loop of 2A & 3A; first abscissa of R_s faint or absent. Hind wing with cell R_1 closed at apex, vein 2A fully developed and joining 1A. Antennae with second segment small and annular, flagellum of male large and flattened, of female swollen.

Contains only one species, whose complete synonymy is presented here for the first time.

Metallus rubi Forbes

Metallus rubi Forbes, 1885, p. 87, ♂.

Metallus rohweri MacGillivray, 1909c, p. 267, ♀. *New synonymy.*

Metallus bethunei MacGillivray, 1914c, p. 366, ♂, ♀.

The larva of this sawfly mines the leaves of blackberry. The color of the mesonotum of the adult varies from rufous through dark brown to black.

Fenusa Leach

Fenusa Leach, 1817, p. 126. Monobasic, genotype.—*Tenthredo* (*Emphytus*) *pumilus* Klug (preoccupied, *nec* *Tenthredo* (*Allantus*) *pumilus* Klug) = *Fenusa pusilla* (Lepeletier).

Kaliosysphinga Tischbein, 1846, p. 79. Monobasic, genotype.—*Kaliosysphinga dohrnii* Tischbein.

Aphadnurus O. Costa, 1859, p. 40. Monobasic, genotype.—*Aphadnurus tantillus* Costa = *Fenusa pusilla* (Lepeletier).

Kaliofenusa Viereck in Smith, 1910, p. 591. Genotype by subsequent designation of Rohwer, 1911b.—*Fenusa ulmi* Sundevall.

Characteristics.—Antennae with 9 segments. Front wings with first abscissa of R_1 atrophied, base of 2A & 3A either present as a semi-sclerotized loop, fig. 209, or absent. Hind wings with cell R_1 open at apex, fig. 259; 2A either entirely atrophied, present for its full length, or in various intermediate conditions. Head thick and rounded in front, as in *Caliroa*, fig. 251.

This genus contains quite a variety of forms. When more species are known by both sexes it may be advisable to subdivide it into subgenera. It has been briefly revised by Ross, 1937a.

Profenusa MacGillivray

Profenusa MacGillivray, 1914c, p. 364. Monobasic, genotype.—*Profenusa collaris* MacGillivray = *Profenusa canadensis* (Marlatt).

Differs from *Fenusa* chiefly in possessing the first abscissa of R_1 , having longer and more slender wings and with vein 2A of the hind wings fully developed.

Profenusa canadensis (Marlatt) new combination

Scolioneura canadensis Marlatt, 1895, p. 235, ♀.

Profenusa collaris MacGillivray, 1914c, p. 364, ♂, ♀. *New synonymy.*

This is the only known species in the genus. The larva mines the leaves of *Crataegus*.

SUBFAMILY CLADIINAE

Characteristics.—Prepectus present, sometimes indistinct. Mandibles bidentate, the inner tooth small, fig. 56. Front wings with M joined to R a short distance before divergence of R_1 , 2r absent, 2A & 3A fused to

1A so that the basal abscissa of the former is a short loop. Hind wings with full complement of veins and cross-veins. Tarsal claws cleft with a short inner tooth.

This group contains a few small genera of uniform habitus. The genera are best characterized by the saws of the female. Rohwer and Middleton (1922) revised the group but several species described a year previously by MacGillivray have never been incorporated into the keys.

The Cladiinae are remarkably similar in many characters to the Nematinae but appear to be a distinct, separate offshoot of the Nematine stem.

KEY TO GENERA

1. Males.....2
Females.....3
2. First three segments of flagellum pectinate, fig. 104.....**Cladius**
First three segments of flagellum not pectinate,
fig. 256.....**Trichiocampus, Priophorus**
3. Third antennal segment strongly compressed bilaterally, short and emarginate beneath, fig. 255.....**Cladius**
Third antennal segment round, long and scarcely emarginate beneath, fig. 256.....4
4. Ventral margin of saw nearly straight, armed with 12-14 serrations, fig. 260.....**Trichiocampus**
Ventral margin of saw concave, armed with 8 large teeth,
fig. 261.....**Priophorus**

Trichiocampus Hartig

Cladius subg. *Trichiocampus* Hartig, 1837, p. 176. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus grandis* Lepeletier = *Trichiocampus viminalis* (Fallén).

Characteristics.—Antennae long, slender, and setaceous, somewhat bilaterally compressed in male, the third segment in the male with a basal projection in some species. Front basitarsus shorter than the three following segments combined. Saw without lateral armature, but with twelve or more segments, fig. 260.

Six described species belong in this genus, but the synonymy has not yet been worked out.

Priophorus Dahlbom

Nematus subg. *Priophorus* Dahlbom, 1835, p. 4. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus (Priophorus) pilicornis* Dahlbom = *Priophorus pallipes*. (Lepeletier).

Stevenia Brullé, 1846, p. 667. No included species.

Characteristics.—Differs from *Trichiocampus* chiefly as follows: third segment of antennae of male never with basal projection, front basitarsus usually subequal to length of three following segments combined and saw with distinct lateral armature and only eight segments, fig. 261.

Contains about fifteen species which are badly in need of revision.

Cladius Rossi

Cladius Rossi, 1807, p. 27. Genotype by subsequent designation of Latreille, 1810.—*Tenthredo difformis* Panzer.

Characteristics.—Antennae of female shorter than in two preceding genera, the third segment short and concave ventrally; of male slender, with third, fourth, and fifth segments pectinate, fig. 104. Front basitarsus equal in length to three following segments combined. Saw similar to that of *Priophorus*, fig. 261.

Contains only one species in North America, *C. isomerus* Norton, which attacks cultivated roses and is probably a synonym of a European one.

SUBFAMILY NEMATINAE

This subfamily has been divided into two or three subfamilies by various authors, but to do so destroys the picture of its composition. The various genera coming within its limits present an almost perfectly intergraded chain of conditions ranging from the most primitive genus, *Hoplocampa*, to a closely knit, specialized group of genera including *Pristiphora*, *Nematus*, and *Euura*.

In *Hoplocampa* the front wings, fig. 191, have 2r present, the basal abscissa of 2A & 3A present and showing the typical angulation, and 3r-m received in cell 3R_s; the mandibles are triangular from a side view, fig. 270; and the penis valves of the genitalia are composed of only one leaf at the apex. Through differences shown in such genera as *Hemichroa*, *Anoplonyx*, and *Platycampus*, these gradually resolve themselves into the following: front wing, fig. 193, with 2r absent, basal abscissa of 2A & 3A absent, and 3r-m received in cell 2R_s; mandibles with dorsal portion concave, appearing blade-like from a side view, fig. 272; and penis valves with apex composed of two leaves, a mesal membranous one and a lateral sclerotized one, fig. 314.

The only exception to this trend is the small group containing *Pseudodineura* and *Kerita*, in which the mandibles are distinctly tridentate, fig. 318. There is slight indication of a beginning of the middle tooth in *Susana* and *Hemichroa*, fig. 317, so that this tridentate mandible apparently marks an early offshoot of the Nematinae.

The higher group of genera must have evolved some highly beneficial biological characteristics, because they are at present the most abundant boreal sawfly group in number of species and probably also in population. Most of them are not large or conspicuously colored, so that they are seldom collected abundantly by the general entomologist, but a close search usually reveals them in numbers. The most valuable paper in dealing with these forms is the revision of Marlatt, 1896b.

KEY TO GENERA

1. Base of vein 2A & 3A present, figs. 200, 202.....2
Base of vein 2A & 3A atrophied, fig. 198.....8
2. Prepectus invisible, apparently wanting.....**Susana**
Prepectus not reduced, triangular and distinct.....3
3. Tarsal claws without an inner tooth, fig. 262.....**Anoplonyx**
Tarsal claws with an inner tooth, either large or small.....4
4. Antennae with second segment longer than wide, subequal in length to eighth, fig. 281.....5
Antennae with second segment wider than long, at most half the length of eighth, fig. 282.....6
5. Tarsal claws bent over a sharp angle near middle, with a long inner tooth, fig. 263. Front wing with 2r absent.....**Caulocampus**
Tarsal claws only gently curved, with a short inner tooth, as in fig. 266. Front wings with 2r present.....**Hoplocampa**
6. Malar space greater than length of first antennal segment, subequal to length of first two combined, fig. 292.....**Platycampus**
Malar space no greater than length of first antennal segment, fig. 291.....7
7. Antennae stocky and approximately of same thickness throughout, fig. 282. Clypeus deeply and circularly incised.....**Craterocercus**
Antennae slender and tapering, fig. 283. Clypeus shallowly or angularly emarginate, fig. 291.....**Hemichroa**
8. Hind wings with vein 2A & 3A present, fig. 287.....10
Hind wings with vein 2A & 3A atrophied, fig. 288.....9
9. Ocelli forming a wide triangle, fig. 294.....**Pseudodineura**
Ocelli forming a flatter triangle, fig. 295.....**Kerita**
10. Front wings with cross-vein 2r present, fig. 285.....11
Front wings with cross-vein 2r atrophied.....12
11. Tarsal claws cleft, with a large inner tooth, fig. 269.....**Adelomos**
Tarsal claws simple, without an inner tooth, fig. 262.....**Neopareophora**
12. Hind basitarsus greatly expanded, fig. 277.....**Croesus**
Hind basitarsus no wider than tibia, fig. 276.....13
13. Front wings with cross-vein 2r-m present, fig. 193.....14
Front wings with cross-vein 2r-m atrophied, fig. 195.....**Euura**
14. Tarsal claws without an inner tooth, fig. 262.....**Pristiphora**
Tarsal claws with an inner tooth, figs. 264-268.....15
15. Males.....27
Females.....16
16. Ninth segment extremely large and wide, ventrally, fig. 293.....**Nematinus**
Ninth segment much shorter or narrower ventrally than fig. 293.....17
17. Tarsal claws with inner tooth either small, appearing as a subtooth of the outer one, fig. 264, or quite a distance from it, fig. 265.....18
Tarsal claws with inner tooth at least approaching outer one in length and more or less parallel with it, figs. 266-268.....23
18. Sheath with lateral face polished, flat and with only microscopic setae....19
Sheath with lateral face either rough, mound-like or with most of its surface covered with conspicuous setae.....20

19. Sheath projecting considerably beyond apex of cerci, fig. 298....**Pikonema**
 Sheath projecting scarcely at all beyond cerci, fig. 304.....**Pristiphora**
20. Inner and outer teeth of tarsal claws forming a more or less semicircular clasp, fig. 265.....**Micronematus**
 Inner tooth of tarsal claws merely a projection at base of outer tooth, fig. 26421
21. Sheath with a definite scopa, or shelf-like lateral process at apex as in figs. 308, 311.....**Pristiphora**
 Sheath without a scopa.....22
22. Clypeus almost truncate, not emarginate on meson, fig. 297.....**Pristiphora**
 Clypeus definitely emarginate on meson, fig. 296.....**Pachynematus**
23. Left mandible seen in lateral view with base bulbous and apical portion long, thin, and blade-like, as in fig. 272.....25
 Left mandible either gradually tapering in width from base to apex, fig. 270, or with the apical portion short and stubby, fig. 273.....24
24. Antennae very long, slender, and markedly tapering, fig. 283....**Hemichroa**
 Antennae shorter, stocky, and at most only slightly tapering, as in fig. 279.....**Euura**
25. Head, figs. 299, 300, with median crest rounding off fairly evenly in lateral view, not hump-like and protuberant.....**Amauronematus**
 Head, figs. 301, 302, with median crest protuberant and somewhat angled in lateral view.....26
26. Sheath with a wide scopa as in fig. 308.....**Pristiphora**
 Sheath without a scopa, at most with the apical margin slightly thickened.....**Nematus**
27. Clypeus emarginate on meson, forming two lateral lobes, fig. 296.....29
 Clypeus not emarginate on meson, fig. 297.....28
28. Penis valve with apical process of lateral flap on dorsal side, fig. 316.....**Nematus**
 Penis valve with apical process of lateral flap not on dorsal side, figs. 313, 314**Pristiphora**
29. Apical sternite wide and emarginate at apex, fig. 306.....30
 Apical sternite either much more narrowed towards apex or not at all emarginate.....31
30. Left mandible tapering fairly regularly from base to apex without a neck-like constriction between base and apical blade, fig. 271.....**Nematinus**
 Left mandible with base bulbous and with a definite narrowing between base and blade-like apex, fig. 272.....31
31. Tarsal claw with inner tooth very small and situated some distance from apex, fig. 264.....32
 Tarsal claw with inner tooth either larger, fig. 265, or situated closer to apex, fig. 266.....33
32. Eighth tergite with a procidentia, i.e., a median, raised process set off from the lateral areas by declivous sides, fig. 324.....**Pikonema**
 Eighth tergite produced or carinate but never with the median process set off from the lateral areas by declivous sides.....**Pachynematus**
33. Left mandible with the narrowed apical portion long, fig. 272.....34
 Left mandible with the narrowed apical portion short and stubby, fig. 273.....**Euura**

34. Tarsal claws with inner tooth situated some distance from apex and curved to form a semicircular clasp with outer tooth, fig. 265.....**Micronematus**
Tarsal claws with inner tooth situated closer to apex, not forming the semicircular outline as above, fig. 266.....35
35. Head, figs. 299, 300, with median crest rounding off fairly evenly in lateral view, not prominently humped.....**Amauronematus**
Head, figs. 301, 302, with median crest protuberant and somewhat angled in lateral view.....36
36. Eighth tergite with small, narrow, and inconspicuous procidentia, fig. 325, and apical sternite very short, bluntly-rounded at apex, fig. 305 **Pristiphora**
Either eighth tergite with a conspicuous, well-differentiated procidentia, as in fig. 324, and the apical sternite produced and more angulate apically.....**Nematus**

Hoplocampa Hartig

Hoplocampa Hartig, 1837, p. 276. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo* (*Allantus*) *brevis* Klug.

MacGillivraya Ashmead, 1898, p. 257. Genotype by original designation.—*MacGillivraya oregonensis* Ashmead. Preoccupied.

Macgillivrayella Ashmead in Smith, 1899, p. 606. New name for *Macgillivraya* Ashmead.

Characteristics.—Small sawflies, usually shorter than 5 mm. Front wings with 2r and base of 2A & 3A present. Antennae fairly short and robust, slightly tapering, the two basal segments together subequal to the third. Tarsal claws with small to medium-sized inner tooth. Malar space variable. Saw without marked transverse bands of setae. Penis valves simple, not divided into mesal and lateral flaps, but sometimes with filamentous lateral processes.

Caulocampus Rohwer

Caulocampus Rohwer, 1912b, p. 239. Genotype.—*Priophorus acericaulis* MacGillivray.

Characteristics.—Similar to *Hoplocampa* in venation and general features. Differs in having the antennae shorter and stockier, and the inner tooth of the tarsal claws large and thick, fig. 263.

Contains only a single species, *C. acericaulis* (MacG.), which mines the petioles of maple leaves.

Susana Rohwer and Middleton

Susana Rohwer and Middleton, 1931, p. 93. Genotype by original designation.—*Susana cupressi* Rohwer and Middleton.

Characteristics.—Front wings with 2r absent or present, 2m-cu joining cell 2R_s or 1R_s, and base of 2A & 3A present. Antennae slender, long and setaceous. Tarsal claws with a moderate inner tooth. Prepectus

reduced to a very thin sclerite, usually invisible, along the antero-dorsal margin.

Contains two nearctic species.

Craterocercus Rohwer

Craterocercus Rohwer, 1911d, p. 385. Genotype by original designation.—*Hemichroa phytophagica* Dyar.

Characteristics.—Venation similar to *Susana*, usually with *2r-m* and *2m-cu* interstitial. Antennae long, slightly robust, and of the same thickness throughout, fig. 282. Clypeus narrow, arcuately emarginate, the lateral lobes pointed and finger-like. Malar space narrow. Saw with transverse rows of spines. Penis valve with lateral flap represented by a broad spine-like process.

This genus contains about eight species, which have been keyed out by Rohwer, 1918d. It is very closely allied to the European genus *Mesoneura*, differing chiefly in possessing the basal abscissa of vein 2A & 3A in the front wing.

Hemichroa Stephens

The two subgenera listed here may ultimately prove to be distinct genera. At the present, however, the male of one is unknown and no good diagnostic character of significance has been discovered for the female. On the other hand there is every evidence that the groups are closely related.

KEY TO SUBGENERA

1. Base of 2A & 3A pigmented and forming a distinct loop, fig. 289 ***Hemichroa***
Base of 2A & 3A unpigmented and forming a smaller loop, fig. 290.... ***Varna***

Subgenus *Hemichroa* Stephens

Hemichroa Stephens, 1835, p. 55. Genotype by subsequent designation of Westwood, 1849.—*Tenthredo alni* Linnaeus.

Leptocerca Hartig, 1837, p. 228. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo alni* Linnaeus.

Engages Gistel, 1848, p. 9. New name for *Leptocerca* Hartig.

Leptocercus Thomson, 1871, p. 76. Emendation of *Leptocerca*.

Characteristics.—Venation too variable to be described other than falling within the subfamily definition. Antennae long and setaceous, fig. 283. Clypeus, fig. 291, wide and angularly emarginate. Malar space short. Tarsal claws with a large inner tooth. Genitalia of both sexes similar to *Craterocercus*.

This subgenus contains only one nearctic species which is probably truly holarctic in distribution. Its full synonymy has not been given heretofore.

Hemichroa crocea (Fourcroy)

Tenthredo crocea Fourcroy, 1785, p. 364.

Dineura americana Provancher, 1882, p. 292. *New synonymy.*

Hemichroa pallida Ashmead, 1890, p. 15. *New synonymy.*

Hemichroa dyari Rohwer, 1918d, p. 171. *New synonymy.*

Hemichroa washingtonia Rohwer and Middleton, 1931, p. 97.

The variant described by Provancher as *Dineura americana* has usually been considered a distinct species close to *crocea*. Three series of females from New York, Quebec, and England show both extremes and the bridging intermediates, so that the differentiation cannot be used.

Subgenus *Varna* new subgenus

Characteristics.—Both mandibles triangular from a lateral view, fig. 270. Front wings with base of vein 2A & 3A either weak or absent, 2m-cu received in cell 1R_s, and r absent; tarsal claws deeply cleft, the inner tooth subequal and subparallel to the outer tooth; clypeus deeply and circularly emarginate; antennae very long, slender, and gradually tapering to apex. Based on female, since no males have yet been described.

Genotype by original designation.—*Nematus militaris* Cresson.

This genus may be separated by means of the accompanying key from those genera of the Nematinae in which the base of vein 2A & 3A is present. Of those genera in which the base of vein 2A & 3A is atrophied, *Varna* most closely resembles *Nematus* in general appearance, but can easily be separated from this latter genus on the basis of the left mandible being triangular, fig. 270, from the lateral aspect. In *Nematus* it is hollowed out dorsally and the lateral aspect is as shown in fig. 272. According to Yuasa's classification of the immature stages, the larva of *Varna* differs from that of *Nematus* in lacking suranal processes on the tenth abdominal tergum.

Varna includes three nearctic species, *thoracicus* (Harrington), *militaris* (Cresson), and *amelanchieridis* (Rohwer) which have formerly been placed in *Nematus* (*Pteronidea*).

Pseudodineura Konow

Dolerus subg. *Pelmatopus* Hartig, 1837, p. 244, preoccupied. Monobasic, genotype.—

Dolerus (*Pelmatopus*) *minutus* Hartig.

Pseudodineura Konow, 1885c, p. 297. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo* (*Allantus*) *parvula* Klug.

Characteristics.—Front wing with 2r present and base of 2A & 3A absent. Hind wing with 2A atrophied, fig. 288. Prepectus typical. Antennae subfiliform, fig. 279. Malar space absent. Right mandible short and uniformly tapering from base to apex, fig. 319, tridentate, the two

inner teeth shorter than in fig. 318. Tarsal claws simple, without an inner tooth. Male abdomen without a procidentia.

The nearctic fauna in this genus is unexplored. To date only one North American species, *parva* (Norton), has been described.

Kerita new genus

Characteristics.—Venation typical of the Nematinae, the front wing, fig. 195, with *2r* present, *2r-m* absent, and the basal loop of 2A & 3A absent; and with the free stem M represented by a minute basal stub. Mandibles tridentate as in fig. 318, the outer tooth largest. Antennae slender and setaceous, fig. 284, the second segment wider than long, the remainder long and diminishing in length only gradually. Ocelli small, fig. 295, grouped together in a low triangle and separated from the eyes by a wide area. Malar space present, almost as long as the second antennal segment. Tarsal claws slender and simple, as in fig. 262.

Genotype.—*Kerita fidala* new species.

This genus represents, with *Pseudodineura*, the end of a small, specialized branch of the Nematinae. The progenitors of this group were probably forms allied to *Hemichroa*. The genus *Kerita* resembles only *Pseudodineura*, from which it differs in the smaller and more compact ocellar triangle, the distinct malar space, and the larger inner teeth on the mandibles. At present it is known only from the genotype.

Kerita fidala new species

Female.—Length 3.75 mm. Color black with the following parts piceous: mandibles, trochanters, femora, tibiae, and base of basitarsus. Wings very slightly smoky, venation brown.

Head and body shining, clothed with sparse setae. Head with ocellar basin absent, represented by a narrow raised area extending from the ocelli to the supraclypeal area, with a slight concavity down the middle. At the anterior end of this raised area is a shallow, sunken, U-shaped area, the median fovea. Clypeus long and wide, its sides sloping and apical margin straight, the apex flat and the base slightly raised. Supraclypeal area hump-like, rising sharply from the clypeus. Thorax robust, scutellum practically flat, with a distinct post-tergite. Sheath slender and blade-like, practically identical with that of *Pseudodineura*, fig. 309. Saw with lance of 10 segments, humped in the middle and tapering to a point at apex; lancet, fig. 310, with 13 segments separated only by faint sutures, each lobe with 6-12 minute teeth, the last tooth produced basad to form a projection on the apical eight segments, the entire surface of the lobate area covered with sparse but conspicuous setae.

Holotype, female.—Muncie (spelled "Munsey" on label), Illinois, April 25, 1914. In the collection of the Illinois State Natural History Survey.

Neopareophora MacGillivray

Neopareophora MacGillivray, 1908a, p. 289. Genotype by original designation.—

Neopareophora martini MacGillivray = *litura* (Klug).

Dineuridea Rohwer, 1912b, p. 240. Monobasic, genotype.—*Marlattia erythrothorax* Rohwer.

Characteristics similar to above with the following distinctions: malar space distinct; antennae long and tapering, fig. 280; mandibles narrow, right one appearing thin and blade-like from lateral view, fig. 275; hind wings with 2A present, fig. 287.

Female with sheath thick, margins shelf-like, with long cerci, figs. 308, 311.

Contains two nearctic species which have been revised by Ross (1935b).

Adelomos Ross

Adelomos Ross, 1935b, p. 201. Genotype by original designation.—*Adelomos cleone* Ross.

Characteristics.—Front wing with 2r present, base of 2A & 3A absent. Hind wings with a radial cross-vein, fig. 286, and with 2A present. Prepectus present, triangular, well defined, and of moderate size. Antennae, fig. 278, almost filiform, the segments of the flagellum distinctly narrower at the base and wider at apex. Right mandible, fig. 274, broad at base with a fairly narrow blade. Tarsal claws cleft, the inner tooth stout and almost as long as the outer, fig. 269.

Includes only the genotype. This form is unique among sawflies in possessing a radial cross-vein in the hind wing.

Anoplonyx Marlatt

Anoplonyx Marlatt, 1896a, p. 18. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus pectoralis* Lepeletier.

Marlattia Ashmead, 1898, p. 287. Genotype by original designation.—*Hoplocampa laricis* Marlatt. *New synonymy*.

Characteristics.—Front wings with 2r present or absent, 2m-cu joining cell 2R_a, basal loop of vein 2A & 3A present. Antennae very slender and setaceous. Tarsal claws without an inner tooth, fig. 262. Saw curved at apex with curved rows of spines on each segment. Penis valves with a mesal membranous flap and a sclerotized, spike-like lateral one.

Anoplonyx and *Marlattia* have more recently been considered as subgenera of *Platycampus* and *Hemichroa* respectively. The two groups were separated on the basis of the presence or absence of the second

radial cross-vein. In *Platycampus sens. st.* this cross-vein is always absent, but in *Hemichroa sens. st.* it may be present or absent. Furthermore, in a series of three specimens of *Anoplonyx laricis* (Marl.), one has 2r absent, one has it weakly developed and the third has it well developed. It is, therefore, impossible to use this character as a basis for separating the genera. The species placed here, however, are allied by such distinctive attributes as simple tarsal claws and a type of saw peculiar within the group.

Anoplonyx occidentis new name

Platycampus (*Anoplonyx*) *laricis* Rohwer and Middleton, 1931, p. 95. Preoccupied by *A. laricis* (Marlatt), 1896b, p. 257.

The merging of *Marlattia* and *Anoplonyx* brings into the same genus the two names *laricis*. Since the later species described by Rohwer and Middleton is a good species it is necessary to give it a new name.

Platycampus Schiödt

Nematus subg. *Leptopus* Hartig, 1837, p. 104, preoccupied. Monobasic, genotype.—

Nematus (*Leptopus*) *hypogastricus* Hartig = *Platycampus luridiventris* (Fallén). *Platycampus* Schiödt, 1839, p. 20. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus* (*Leptopus*) *hypogastricus* Hartig = *Platycampus luridiventris* (Fall.)

Erasminus Gistel, 1848, p. IX. New name for *Leptopus* Hartig.

Camponiscus E. Newman, 1869, p. 215. Monobasic, genotype.—*Camponiscus healaei* E. Newman = *Platycampus luridiventris* (Fallén).

Characteristics.—Front wings with base of 2A & 3A present as a distinct loop, but 2r absent. Mandible triangular from a side view. Antennae long and setaceous. Malar space very wide, greater than length of first antennal segment. Tarsal claws with a large inner tooth. Saw with indistinct lateral armature.

The species *juniperi* Rohwer, originally described in *Platycampus*, belongs in *Susana*. The removal of this species and *Anoplonyx* from *Platycampus* leaves a residue of four described nearctic species which form a compact genus. The specific status of the species is indefinite.

Nematinus Rohwer

Nematinus Rohwer, 1911b, p. 99. Genotype by original designation.—*Tenthredo abdominalis* Panzer.

Characteristics.—Front wings with both 2r and base of 2A & 3A atrophied. Mandibles representing an intermediate condition between the tapered and blade-like types, fig. 271. Antennae long and setaceous. Tarsal claws with a small inner tooth. Female with segment at base of sheath extremely large and broad at base, fig. 293. Male with no en-

largement of apex of abdomen, eighth tergite produced into a broad, rounded lobe on meson, fig. 326, and with apical sternite emarginate, fig. 306.

Male.—Length 6 mm. Color brownish yellow with the following parts piceous or black: two basal segments of antennae; a large, diamond-shaped mark on ocellar region, reaching from eye to eye and antennae to back of head; posterior aspect of head; praescutum and scutum; mesopectus; and some indefinite blotches on the metanotum and first abdominal tergite. Wings stained with brown basad of stigma; beyond they are hyaline; venation brownish yellow.

General structure as given under genus. Penis valve, fig. 315, with mesal and lateral flaps not differentiated, but with apex divided into two small, membranous lobes and lateral face with a sclerotized spur. This is the spur which later tips the lateral flap in the more specialized genera.

Allotype, male.—Hampton, N. H., June 5, 1908, S. Albert Shaw. In the collection of the Illinois State Natural History Survey.

Several species, such as *chloreus* (Norton), have been incorrectly placed in this genus. When restricted according to the above diagnosis, it contains four or five very closely related if not identical species in the nearctic region.

Specialized Nematinae

The genera treated below form the "blossom" of the Nematine stem. Many are difficult to separate in a key but at the same time obviously form distinct phylogenetic groups. Large numbers of species are involved so that it was felt that as many phylogenetic units should be considered genera as possible. The plan followed has been simple—if key characters were found the groups were given generic rank, if not, subgeneric rank.

The entire assemblage has the following characters in common except where noted: front wings with 2r and base of 2A & 3A atrophied, fig. 193; right mandible with base bulbous and apex slender and blade-like, fig. 272; antennae setaceous, with the two basal segments short.

This entire group of genera is in chaotic condition taxonomically. The conventional specific differences of head sculpture and body color, etc., are entirely inadequate for the task. Detailed studies of genitalia and larval characters will be the very least that can be used in the future.

Pristiphora Latreille

Characteristics.—Clypeus usually truncate, fig. 297, in a few species decidedly emarginate. Tarsal claws varying from simple to possessing a medium sized tooth. Head with lateral walls of ocellar basin usually absent, at most merely indicated as ridges; the ocellar basin itself usually absent and represented by an area raised above the level of the surround-

ing areas. Front wings with first abscissa of R_s frequently atrophied. Genitalia of both sexes variable.

Judging by the male genitalia, this genus is the oldest of the specialized Nematinae. This is indicated first by the extreme differences evolved in the male genitalia and secondly that what might be considered as the generalized type of *Pristiphora* has a penis valve with the tooth of its lateral flap dorsal, whereas it is ventral in the others. There appear to be some distinct phylogenetic groups within the genus but a more detailed study of both nearctic and exotic species is necessary to bring out their worth as genera. Three of these are here classed as subgenera on the basis of genitalia.

SYNOPSIS OF SUBGENERA

1. Male with apex of eighth tergite with a fan-shaped mesal area which is either convex or somewhat carinate. Penis valves various, but not as in fig. 313. Female saw either with a "scopa" or pointed and subtriangular, its sides usually coarsely punctured. Tarsal claws various....***Pristiphora***
2. Male with apex of eighth tergite possessing a small, tapering procidentia, fig. 325. Penis valve with apical spur bent at right angles to valve, fig. 313. Female sheath provided with a distinct scopa. Tarsal claws with a moderate inner tooth.....***Sala***
3. Male with apex of eighth sternite fan-shaped, but with a definite, narrow procidentia which is not produced beyond the apex of the segment. Female saw with a distinct scopa, differing from those of *Pristiphora* s. st. in having the disto-ventral margin incised so that the apex is pointed. Tarsal claws simple.....***Gymnonychus***

Subgenus *Pristiphora* Latreille

Pristiphora Latreille, 1810, p. 294. Genotype by original designation.—*Pteronous testaceus* Jurine.

Diphadnus Hartig, 1837, p. 225. Monobasic, genotype.—*Nematus fuscicornis* Hartig = *Pristiphora pallipes* (Lepeletier).

Lygaeonematus Konow, 1890, p. 238. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus pini* Retzius = *Pristiphora abietinus* Christ.

Neotomostethus MacGillivray, 1908a, p. 290. Genotype by original designation.—*Neotomostethus hyalinus* MacGillivray. *New synonymy*.

This group contains some thirty or forty described North American species. The genus *Neotomostethus* was originally described in the Blennocampinae but its genotype is obviously a typical *Pristiphora*.

The gooseberry sawfly is referred to unanimously in North American economic literature as *Diphadnus appendiculatus* Hartig but it should be called *Pristiphora pallipes* (Lep.). This synonymy has been recognized by European authors for many years.

Subgenus *Gymnonychus* Marlatt

Gymnonychus Marlatt, 1896a, p. 122. Genotype by original designation.—*Gymnonychus californicus* Marlatt.

Contains only one known species, the genotype.

Subgenus *Sala* new subgenus

Characteristics.—Clypeus emarginate. Antennae long and tapering. Dorsal portion of head without distinct ridges, ocellar basin represented by a raised area with sloping boundaries. Frontal crest raised and appearing somewhat angulate from side view, as in fig. 302. Depressions between eyes and antennal sockets neither very deep nor extending much above antennae. Tarsal claws with a long inner tooth subparallel with outer one, as in fig. 269. Female sheath with a scopa set off by a deep depression. Male with apical sternite round and short, fig. 305; eighth tergite with a narrow procidentia, fig. 325; and lateral flap of penis valve with a dorsal tooth bent over at right angles to the axis of the shaft, fig. 313.

Genotype by original designation.—*Nematus chloreus* Norton.

The genotype has been described or placed in both *Nematinus* and *Nematus* (*Pteronidea*) but it does not belong in these genera. Its only ally is *Pristiphora*, in which it seems to form a quite distinct subgroup.

Pristiphora chlorea (Norton) new combination

Nematus chloreus Norton, 1867, p. 221, ♀.

Nematus pallifrons Cresson, 1880, p. 6, ♂. *New synonymy*.

Pteronus quercus Marlatt, 1896a, p. 67, ♀. *New synonymy*.

This species feeds on oak, and is distributed from New York to Texas. I have examined the types of the three names involved. Another species described as *Amauronematus vaculus* MacGillivray from Oregon is either another synonym or a very closely allied species.

Pachynematus Konow

Pachynematus Konow, 1890, p. 238. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus capreae* Panzer = *Pachynematus trisignatus* (Förster).

Characteristics.—Clypeus emarginate. Tarsal claws with a very small tooth situated some distance from apex of outer tooth, fig. 264. Frontal crest and lateral boundaries of ocellar basin sharp, although sometimes low. Female sheath never with scopa, tapering to a pointed apex. Male with apical sternite always at least somewhat produced; eighth tergite either with a carina-like procidentia or a long, convex produced one, penis valve with the tooth of the lateral flap ventral.

Contains 30 or 40 described species from North America. The association of the two sexes of many species is not known, and indicates the need for intensive study of the genus. The larvae of most of the species of this genus differ from those of all related genera in feeding on grasses and sedges and in having the posterior end of the body markedly tapering and pointed.

Micronematus Konow

Micronematus Konow, 1890, p. 239. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus pullus* Förster = *Micronematus monogyniae* (Hartig).

Very similar to *Pachynematus*, differing chiefly as follows: Size small, 4-5 mm. Inner tarsal claw tooth large, so that the two teeth form a C-shaped arc, fig. 265. Female sheath short, its ventral margin evenly rounded. Male with apical sternite tapering to a narrow, round tip; eighth tergite with a narrow, carinate procidentia which projects beyond the margin of the segment.

Contains one nearctic species, *gregarius* (Marlatt).

Micronematus gregarius (Marlatt)

Pachynematus gregarius Marlatt, 1896b, p. 256, ♂, ♀.

Pachynematus rarus MacGillivray, 1921a, p. 30, ♀. *New synonymy.*

Yuasa (1923) first pointed out the placement of this species in *Micronematus* on the basis of larval characters. The larvae feed gregariously on *Salix*.

Pikonema new genus

Similar in general structure to *Pachynematus*, differing as follows: Female sheath long, polished and projecting considerably beyond cerci, fig. 298. Male apical sternite, long, apex tapered to a semi-truncate point, fig. 307; eighth tergite with a procidentia projecting beyond segment, fig. 324.

Genotype by original designation.—*Nematus dimmockii* Cresson.

A compact genus of five species feeding on spruce.

Nematus Panzer

Characteristics.—Clypeus emarginate. Tarsal claws with a large inner tooth subparallel with outer, figs. 267, 268. Head with ocellar basin distinct and usually with well defined lateral walls. Frontal crest appearing angulate from lateral view, fig. 301. Depressions between eyes and antennal sockets not so deep or long as in *Amauronematus*.

The genus has hitherto been considered as three or four separate ones. There seem to be no constant adult, larval, or biological differences, at least none that coincide with each other. For this reason these groups are considered here as subgenera, with no effort to give absolute diagnostic differences between them.

SYNOPSIS OF SUBGENERA

1. Large species, usually over 9 mm. in length, with outer side of hind tibia and basitarsus markedly grooved, fig. 276. Antennae long and setaceous.....**Nematus**
2. Medium to small species with outer side of hind tibiae usually convex or without such a distinct groove as in fig. 276. Antennae always long and setaceous in both sexes. Larvae not inhabiting leaf-curls or galls except in early instars.....**Pteronidea**

3. Small species, usually less than 5 mm. in length, with hind tibiae only indistinctly grooved. Antennae almost always filiform in female, frequently markedly setaceous in male. Larvae inhabiting leaf-curls or galls for their entire life.....**Pontania**

The entire genus contains about 200 described nearctic species. When a thorough study of the males is made it will probably be possible to define the subgenera in terms of male genitalia. All the groups are very imperfectly understood at present.

Subgenus *Nematus* Panzer

Nematus Panzer, 1801, Heft 82, pl. 10. Monobasic, genotype.—*Tenthredo* (*Nematus*) *lucida* Panzer.

Hypolaepus Kirby, 1882, p. 324. Monobasic, genotype.—*Hypolaepus abbottii* Kirby. New synonymy.

Holcocneme Konow, 1890, p. 238. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo crassa* Fallén.

Contains only three or four nearctic species.

Subgenus *Pteronidea* Rohwer

Pteronidea Rohwer, 1911b, p. 98. Genotype by original designation.—*Nematus ventralis* Say.

This contains the larger proportion of the species in the genus. Later studies on genitalia will undoubtedly show that it is composed of several distinct phylogenetic groups.

Subgenus *Pontania* O. Costa

Pontania O. Costa, 1859, p. 20. Genotype by subsequent designation of Marlatt, 1896a.—*Nematus gallicola* Stephens.

Members of this subgenus have been confused with those of *Euura*, since the venation of *Euura* is variable and the two have been separated hitherto on this basis. *Pontania* contains some 40 or 50 described nearctic species.

Genus *Euura* E. Newman

Euura E. Newman, January, 1837, p. 259. Genotype by subsequent designation of Rohwer, 1911b.—*Euura gallae* Newman.

Nematus subg. *Cryptocampus* Hartig, March, 1837, p. 221. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus* (*Cryptocampus*) *medullaris* Hartig.

Characteristics.—Essentially similar in general appearance to *Nematus* subg. *Pontania*. Head with ocellar basin sometimes indistinct, antennae usually filiform. Front wings usually with *2m-cu* absent. Differs from all related genera in having the blade of the left mandible shortened and stubby, fig. 273. Larvae of all species form leaf, petiole, or stem galls on willow.

Several species possessing this abbreviated mandible have in addition the cross-vein *2r-m*, which has led to their description in *Pteronidea* and

Pontania; these it is necessary to remove to *Euura*. Among these are the following known to me:

<i>Pontania gracilis</i> Marlatt	<i>Pontania pisum</i> Walsh
<i>Pontania kincaidi</i> Marlatt	<i>Pontania pomum</i> Walsh
<i>Pontania pacifica</i> Marlatt	<i>Pteronius kincaidi</i> Marlatt

Euura hoppingi new name

Pteronius kincaidi Marlatt, 1896a, p. 55; ♂, ♀. Preoccupied in *Euura* by *Pontania kincaidi* Marlatt.

Croesus Leach

Croesus Leach, 1817, p. 129. Monobasic, genotype.—*Tenthredo septentrionalis* Linnaeus.

Characteristics.—Apparently very closely related to *Nematus* differing from it and other Nematinae, however, in the expanded and foliaceous hind basitarsus and apex of hind tibiae, fig. 277.

Contains only three recorded species from North America. The larvae are extremely similar to those of *Nematus* and indicate a close relationship between them.

Amauronematus Konow

Amauronematus Konow, 1890, p. 237. Genotype by subsequent designation of Rohwer, 1911b.—*Nematus fallax* Lepeletier.

Pontoprastia Malaise, 1921, p. 12. Genotype by present designation.—*Pontoprastia suavis* var. *fusca* Malaise. *New synonymy*.

Characteristics.—Clypeus emarginate. Antennae slender and setaceous. Head with frontal crest appearing evenly convex from lateral view, fig. 299; ocellar basin usually without distinct antero-lateral corners; depressions between eyes and antennal sockets deeper, longer, and situated closer to eye than in *Nematus*. Tarsal claws with a large inner tooth subparallel with outer one.

This genus is a large one, containing forty or fifty species.

SUBFAMILY ALLANTINAE

Prepectus absent. Propleurae with mesal margins either pointed and not approximate, fig. 155, or truncate and meeting, fig. 158. Front wings, fig. 186, with M parallel with 1m-cu and meeting radial stem near origin of R₄; a present. Mesopost-tergite triangular and well developed. Mandibles various.

KEY TO GENERA

1. Mesonotum and pectus entirely covered with thick coarse punctuation.....*Pseudosiobla*
- Mesonotum and pectus with large areas at most with small punctures which are not confluent.....2

2. Mesopleurae entirely covered with close, crater-like punctures, fig. 329....3
Mesopleurae finely striate or with only small punctures.....4
3. Praescutum with anterior portion of each half prominently raised, the posterior portion flat, fig. 331.....**Eriocampa**
Praescutum with each half almost evenly convex over its entire length, fig. 330.....**Dimorphopteryx**
4. Abdomen with a pair of more or less oval, opalescent areas on the five or six basal tergites, giving it a unique, fenestrated appearance, fig. 340.....**Empria**
Abdomen without such areas.....5
5. Malar space narrow, shorter than length of second antennal segment, fig. 334, and propleurae acute and not meeting on meson, fig. 155.....**Phrontosoma**
Either malar space longer than length of second antennal segment, or propleurae truncate and meeting on meson, fig. 158.....6
6. Hind basitarsus at least one and one-third times as long as the remainder of the tarsal segments together, fig. 347.....7
Hind basitarsus subequal to or shorter than remainder of tarsal segments together, fig. 348.....8
7. First abscissa of R_2 atrophied, fig. 186.....**Macremphytus**
First abscissa of R_2 present, see fig. 170.....**Taxonus**
8. First abscissa of R_2 atrophied, fig. 186.....9
First abscissa of R_2 present, see fig. 170.....10
9. Anterior margin of clypeus circularly emarginate for one-half its mesal length, fig. 327.....**Allantus**
Anterior margin of clypeus emarginate for only a third or less of its length, and the incision forming a flatter arc, figs. 320, 322...**Ametastegia** in part.
10. Anal cross-vein nearly transversely placed across the anal cell, fig. 337.....**Ametastegia** in part.
Anal cross-vein sloping more, as in fig. 338.....11
11. Clypeus, fig. 328, narrow, its anterior margin incised to form narrow lateral tips.....**Aphilodactylum**
Clypeus, figs. 332, 333, wide, the incision either shallow or angled to form wide, obtuse lateral portions.....12
12. Hind tarsal segments almost cylindrical, fig. 345; together almost equal in length to the hind tibia.....**Monosoma**
Hind tarsal segments considerably wider at apex and tapering to base, fig. 346; together only two-thirds the length of the hind tibia...**Monostegia**

The genus *Empria* probably represents the most generalized member of the subfamily. The other genera may be grouped around it into three tribes, as follows:

(1) *Allantini*. A regular series of genera lead from *Empria*, through *Monostegia*, *Monosoma*, *Ametastegia*, *Aphilodactylum*, and *Allantus* to the two most specialized genera of the group, *Macremphytus* and *Taxonus*. These latter two differ from *Empria* in having the propleurae truncate and approximate on the meson, fig. 158, the right mandible re-

duced to a unidentate hook, fig. 49, and the praeputial processes incised to form narrow apical lobes, fig. 343.

(2) *Phrontosomini*, including only one nearctic genus, *Phrontosoma*, characterized by the very narrow malar space, and the very small, low praeputial processes in the male genitalia. In other respects the genus is quite generalized, and it is difficult to place it phylogenetically.

(3) *Eriocampini*, including *Pseudosiobla*, *Eriocampa*, and *Dimorphopteryx*. These three genera are grouped together chiefly on the rugose mesopleurae, but differ radically from each other in mandibular and antennal structure and genitalia. The praeputial lobes of the genitalia, fig. 341, resemble those of *Empria*, fig. 342, to some extent and probably indicate that these three genera are aberrant offshoots of an early stem.

Empria Lepeletier

This genus contains seven nearctic species revised by Ross, 1936b. They are separated on the basis of saws and male genitalia, and grouped into two subgenera.

KEY TO SUBGENERA

Head entirely black.....	<i>Empria</i>
Head with inner orbits yellow.....	<i>Parataxonus</i>

Subgenus *Empria* Lepeletier

Empria Lepeletier, 1828, p. 571. Genotype by subsequent designation of Brullé, 1846.—*Dolerus* (*Empria*) *pallimacula* Lepeletier.

Poecilostoma Dahlbom, 1835, p. 13. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo guttatum* Fallén.

Prosecria Gistel, 1848, p. X. New name of *Poecilostoma*.

Poecilosoma Thomson, 1871, p. 227. Emended spelling of *Poecilostoma*.

Poecilostomidea Ashmead, 1898, p. 256. Genotype by original designation.—*Emphytus maculatus* Norton.

Tetratneura Ashmead, 1898, p. 256. Genotype by original designation.—*Selandria ignotus* Norton.

Empria subg. *Triempria* Enslin, 1914, p. 213. Genotype by original designation.—*Empria tridens* Konow.

Both mandibles bidentate, as in fig. 51. Propleurae with mesal angles pointed and not approximate, fig. 155. Clypeus with a median keel, variuously incised, fig. 323. Antennae variable. Front wings with a oblique, first abscissa of R₁ present or absent. Abdomen with at least the four or five basal segments bearing a pair of opalescent areas, fig. 340.

Subgenus *Parataxonus* MacGillivray

Parataxonus MacGillivray, 1908b, p. 367. Genotype by original designation.—*Taxonus multicolor* Norton.

Leucempria Enslin, 1913, p. 187. Genotype by original designation.—*Tenthredo candidula* Fallén. New synonymy.

Differs from *Empria s. st.* in having the clypeus, fig. 321, with a wide, angular incision forming triangular lobes, and without a median keel; also in having a peripheral vein around the hind wing in the male, fig. 180.

Monostegia O. Costa

Monostegia O. Costa, 1859, p. 60. Genotype by subsequent designation of MacGillivray, 1908b.—*Tenthredo abdominalis* Fabricius.

Clypeus wide and only moderately emarginate, fig. 333. Hind tarsi only two-thirds the length of the hind tibiae, each segment wider at apex and tapering to base, fig. 346. Propleurae with mesal margins slightly truncate. Antennae with third segment almost as long as third and fourth together. Venation similar to *Empria*. Abdomen without opalescent areas.

This genus is closely related to *Empria* and is considered a subgenus of it by Enslin and others. It is represented in North America by only a single holarctic species, *abdominalis* (Fabr.), which has two synonyms hitherto unrecorded in North American literature.

Monostegia abdominalis (Fabricius)

Tenthredo abdominalis Fabricius, 1798, p. 216.

Monostegia martini MacGillivray, 1908b, p. 366, ♀. *New synonymy.*

Monostegia nearctica Rohwer, 1912b, p. 209, ♂, ♀. *New synonymy.*

The only nearctic records for this species are along the Atlantic coast.

Monosoma MacGillivray

Monsoma MacGillivray, 1908b, p. 368. Genotype by original designation.—*Taxonius inferentia* Norton.

Monosoma Viereck in Smith, 1910, p. 583. Emended spelling of *Monsoma*.

Judging from MacGillivray's later papers and by his handwritten labels in his collection, the original spelling "*Monsoma*" was a *lapsus calami* and the emended spelling should stand.

Hind tarsi almost as long as hind tibiae, fig. 345, the segments almost cylindrical. Front wing with distal anal cell short, narrow, and sharply triangular, fig. 339. Clypeus wide and only moderately emarginate, fig. 332. Propleurae with mesal portion wide and almost truncate. Antennae with third segment subequal to length of fourth and fifth together.

Ametastegia A. Costa

The nearctic species of this and the following two genera have been revised by Ross (1937b). In common with other genera of the subfamily, they contained a great many synonymous names and misplacements.

KEY TO SUBGENERA

Front wings with first abscissa of R_2 present.....*Ametastegia*
Front wings with first abscissa of R_2 absent.....*Prottemphytus*

Subgenus *Ametastegia* A. Costa

Ametastegia A. Costa, 1882, p. 198. Monobasic, genotype.—*Ametastegia fulvipes* A. Costa = *Ametastegia glabrata* (Fallén).

Aomodyctium Ashmead, 1898, p. 309. Monobasic, genotype.—*Strongylogaster abnormis* Provancher = *Ametastegia glabrata* (Fallén).

Unitaxonus MacGillivray, 1921b, p. 32. Genotype by original designation.—*Unitaxonus repentinus* MacGillivray = *Ametastegia equiseti* (L.).

Clypeus only slightly or moderately emarginate, figs. 320, 322, the corners sharp. Mandibles, fig. 51, both bidentate. Antennae long. Front wings with *a* almost perpendicular, distal anal cell shorter than proximal anal cell beyond constriction; first abscissa of *R*₁ present; hind wings with both *3r-m* and *m-cu* always lacking. Head with walls of ocellar basin mound-like and not linear. Male genitalia with praeputial processes triangular, fig. 335, penis valve without "shelves" in dorsal portion.

Subgenus *Protemphytus* Rohwer

Protemphytus Rohwer, 1909, p. 92. Monobasic, genotype.—*Emphytus coloradensis* Weldon.

Emphytina Rohwer, 1911d, p. 399. Genotype by original designation.—*Emphytina pulchella* Rohwer = *Ametastegia recens* (Say).

Simplemphytus MacGillivray, 1914c, p. 363. Monobasic, genotype.—*Simplemphytus pacificus* MacGillivray = *Ametastegia tener* (Fallén).

Differs from *Ametastegia* in having the first abscissa of *R*₁ absent in front wings, and in having shelf-like folds in the dorsal portion of the penis valves.

Aphilodictium Ashmead

Aphilodictium Ashmead, 1898, p. 310. Genotype by original designation.—*Strongylogaster rubripes* Cresson = *Aphilodictium fidum* (Cresson).

Polytaxonus MacGillivray, 1908b, p. 368. Genotype by original designation.—*Taxonus robustus* Provancher = *Aphilodictium fidum* (Cresson).

Clypeus narrow and deeply emarginate, the two corners forming short, triangular processes, fig. 328. Mandibles bidentate. Mesal portion of propleurae narrowly truncate and approximate. Antennae slender, segments of flagellum gradually diminishing in length. Front wings with *a* oblique, and *R*₁ entire, hind wings with *3r-m* and *m-cu* absent. Male genitalia with apex of praeputial lobes forming more or less definite, narrowed projections, fig. 336.

Contains only one nearctic species, *fidum* (Cresson), whose synonymy has been discussed by Ross (1937b).

Allantus Panzer

Allantus Panzer, 1801, Heft 82, pl. 12. Monobasic, genotype.—*Tenthredo (Allantus) togatus* Panzer.

Emphytus Klug, 1818, p. 273. Genotype by subsequent designation of Curtis, 1833.—*Tenthredo cinctus* (Linnaeus).

Clypeus deeply, circularly emarginate, often with a ridge around the edge, fig. 327. Right mandible bidentate, left one unidentate, fig. 50. Propleurae with mesal portion truncate. Antennae long and slender, slightly bilaterally compressed in male. Front wings with first abscissa of R_s absent, a oblique and cell DA subequal to cell PA beyond constriction. Hind wings $3r-m$ and $m-cu$ absent. Abdomen black except for a transverse white band on the fifth tergite of the female. Hind basitarsus slightly shorter than remainder of tarsal segments together, fig. 348.

The four nearctic species have been revised by Ross (1937b).

Macremphytus MacGillivray

Macremphytus MacGillivray, 1908b, p. 368. Genotype by original designation.—*Harpiphorus varianus* Norton.

Differs from *Allantus* in having the antennae either moderately or strongly bilaterally compressed in both sexes, $m-cu$ usually present in the hind wing, and the hind basitarsus one and a third times as long as the segments beyond it together. Antennae usually bicolored.

There are nine described nearctic species, including some synonyms.

Taxonus Hartig

Taxonus Hartig, 1837, p. 297. Genotype by subsequent designation of Konow, 1896c.—*Tenthredo* (*Allantus*) *nitida* Klug = *Taxonus agrorum* (Fallén).

Ermilia O. Costa, 1859, p. 106. Monobasic, genotype.—*Ermilia pulchella* O. Costa = *Taxonus agrorum* (Fallén).

Strongylogastroidea Ashmead, 1898, p. 308. Genotype by original designation.—*Strongylogaster apicalis* Say.

Parasiobla Ashmead, 1898, p. 308. Genotype by original designation.—*Strongylogaster rufocinctus* Norton.

Hypotaxonus Ashmead, 1898, p. 311. Genotype by original designation.—*Strongylogaster pallipes* Say.

Clypeus deeply emarginate, the lateral angles produced into finger-like tips except in *epicera*. Left mandible with outer tooth cleft to give appearance of a tridentate condition, figs. 47, 49, right mandible unidentate. Antennae cylindrical. Front wings with R_s entire, a oblique. Hind wing with $3r-m$ and $m-cu$ present or absent; in male with a peripheral vein, fig. 180, partially or entirely lost in one or two species. Hind basitarsus one and one-third times as long as the following segments together.

Phrontosoma MacGillivray

Phrontosoma MacGillivray, 1908b, p. 366. Genotype by original designation.—*Phrontosoma atrum* MacGillivray.

Body short and robust. Clypeus, fig. 334, incised to form rounded lateral lobes. Propleurae with mesal angles narrow and sharp, fig. 155. Antennae, as in fig. 349, short and stout, third segment as long as the two

following together, the apical six almost subequal to each other. Front wings with R_2 entire, a oblique. Hind wing with $3r-m$ absent, $m-cu$ present.

Only a single species is known, *belfragei* (Cresson). The new synonymy connected with it is presented here.

Phrontosoma belfragei (Cresson) new combination

Selandria belfragei Cresson, 1880, p. 15, ♀.

Caliroa nortonia MacGillivray, 1894, p. 324, ♂. *New synonymy.*

Phrontosoma atrum MacGillivray, 1908b, p. 367, ♂. *New synonymy.*

Phrontosoma daeckei MacGillivray, 1908b, p. 367, ♀. *New synonymy.*

Phrontosoma collaris MacGillivray, 1908b, p. 367, ♀. *New synonymy.*

The body of the male is entirely black, of the female either black or with the mesonotum or mesopleurae and mesonotum rufous. The range of the species is extensive, records having been assembled for the following states: Alberta, Illinois, Iowa, Kansas, New York, Ontario, Pennsylvania, Quebec, and Texas.

Eriocampa Hartig

Eriocampa Hartig, 1837, p. 279. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo ovata* Linnaeus.

Mesopleurae with large, adjacent, crater-like punctures. Mesonotum and sternum polished and almost impunctate. Praescutum with anterior half prominently raised, posterior portion flat. Mandibles both unidentate. Propleurae only slightly truncate on meson. Clypeus only slightly emarginate.

Contains two or three nearctic species.

Dimorphopteryx Ashmead

Dimorphopteryx Ashmead, 1898, p. 308. Genotype by original designation.—*Strongylogaster pinguis* Norton.

Differs from *Eriocampa* chiefly in having the praescutum evenly convex for its entire length, the mesonotum coarsely punctured, and the mandibles bidentate. The genus was revised by Rohwer (1915a).

Pseudosiobla Ashmead

Pseudosiobla Ashmead, 1898, p. 308. Genotype by original designation.—*Macrophya excavata* Norton.

Entire head and thorax with large, adjacent punctures. Propleurae with mesal portion thin and angular. Clypeus only very shallowly emarginate.

Contains three nearctic species.

SUBFAMILY BLENNOCAMPINAE

Characteristics.—Front wing, fig. 190, with M joining R at point of separation of R₁, 2r present, M parallel with 1m-cu except in a few cases, 2A & 3A with basal abscissa either very faint, fig. 206, or atrophied beyond bend, figs. 208, 210. Hind wings with venation variable. Prepectus present or absent. Mandibles bidentate. Cervical sclerites pointed and not appressed on meson.

Rohwer divides this group into two, using as the primary difference the presence or absence of the prepectus. It is plain, however, that the prepectal suture is highly unstable in the Blennocampinae. In *Paracharactus rudis* (Norton) it may be either entirely absent or well developed as a furrow. In such closely allied genera as *Phymatocera* and *Rhadinoceraea* it is present in one and not in the other.

Almost all the species in this subfamily are robust, short, and stocky. Approximately a hundred nearctic species have been described but such is the state of keys and literature that three-quarters of them are either synonyms or placed in the wrong genus. The separation of genera is difficult due to a lack of outstanding characters upon which to base phylogeny. It is hoped that future studies of both adults and larvae will bring to light more significant structures.

KEY TO GENERA

1. Antennae conspicuously serrate as in fig. 355.....**Ceratulius**
Antennae either not or only slightly serrate.....2
2. Front wings with M and 1m-cu markedly divergent, fig. 188.....**Tomostethus**
Front wings with M and 1m-cu not markedly divergent, fig. 190.....3
3. Last four antennal segments much shorter than fifth and together only as long as third, fig. 351.....**Waldheimia**
Last four antennal segments either subequal to fifth or together much longer than third.....4
4. Front wing with stub of 2A & 3A furcate at apex, fig. 359.....5
Front wing with stub of 2A & 3A not furcate at apex, figs. 358, 360.....7
5. Head and abdomen black, thorax rufous.....**Paracharactus**
Body unicolorous, black or piceous.....6
6. Prepectus present.....**Phymatocera**
Prepectus absent.....**Rhadinoceraea**
7. Prepectus present.....8
Prepectus absent.....10
8. Third and fourth antennal segments subequal, fig. 354.....**Paracharactus**
Third antennal segment at least one and one-half length of fourth, fig. 349.....9
9. Prepectus flat and triangular, set off by a suture, fig. 361.....**Tethida**
Prepectus raised and shoulder-like, set off by a deep furrow, fig. 362.....**Eutomostethus**
10. Front wing with stub of 2A & 3A turned up at apex, fig. 358.....16
Front wing with stub of 2A & 3A straight at apex, fig. 360.....11

11. Fourth and fifth antennal segments not noticeably longer or thicker than sixth to ninth, fig. 356.....12
 Fourth and fifth antennal segments noticeably longer and thicker than sixth to ninth, fig. 352.....**Waldheimia**
12. Third and fourth antennal segments of same length, fig. 354.....13
 Third antennal segment longer than fourth, fig. 350.....15
13. Antennae with seventh and eighth segments less than twice as long as wide, fig. 356.....**Rhadinoceraea**
 Antennae with seventh and eighth segments much longer than twice width, fig. 354.....14
14. Tarsal claws with a long but slender, inner tooth, fig. 357.....**Claremontia**
 Tarsal claws without an inner tooth.....**Paracharactus**
15. Malar space as narrow as width of tibial spur, fig. 367.....**Blennocampa**
 Malar space wider than width of tibial spur, figs. 365, 366.....16
16. Posterior orbits with a row of large punctures along posterior margin of eye, fig. 370.....**Valco**
 Posterior orbits smooth or only finely punctate along posterior margin of eye.....17
17. Antennae with third and fourth segments subequal in length, fig. 353....18
 Antennae with third segment markedly longer than fourth, fig. 350.....19
18. Eyes removed almost their own length from dorso-caudal margin of head, fig. 365.....**Lagonis**
 Eyes less than half their length from dorso-caudal margin of head, fig. 366.....**Periclista**
19. Tarsal claws simple.....20
 Tarsal claws with a distinct inner tooth.....**Periclista**
20. Eyes small, removed a considerable distance from dorso-caudal margin of head, fig. 369.....**Valco**
 Eyes large, close to dorso-caudal margin of head, fig. 368.....**Pareophora**

Tomostethus Konow

Tomostethus Konow, 1886, p. 184. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo nigrita* Fabricius.

Characteristics.—Front wings with M markedly divergent from 1m-cu, and base of 2A & 3A represented by a faint, sinuate line, fig. 206. Head with malar space practically obsolete, reduced to a thin line. Antennae stocky and filiform, with third segment as long as fourth and fifth together, four to nine gradually decreasing in length. Prepectus triangular, different in texture to episternum. Tarsal claws simple. Sheath short and expanded laterally at apex.

Contains only one described nearctic species, *multicinctus* Rohwer.

Tethida new genus

Characteristics.—Front wings with M parallel with 1m-cu, base of 2A & 3A with apex practically indistinguishable. Malar space, antennae, and sheath as in *Tomostethus*. Prepectus, fig. 361, unusually

large, shining, of same texture as episternum and set off by a line-like suture. Tarsal claws with a short, stocky inner tooth near base.

Genotype by original designation.—*Tenthredo cordigera* Beauvois.

Tethida cordigera (Beauvois) new combination

Tenthredo cordigera Beauvois, 1805, p. 97, ♀.

Tenthredo bardus Say, 1836, p. 218, ♀.

Selandria dubia Cresson, 1865, p. 244, ♀.

This is the only known species in the genus. The application of *cordigera* to this species was pointed out by Dalla Torre in 1895 but has not been followed by North American students.

Eutomostethus Enslin

Tomostethus subg. *Eutomostethus* Enslin, 1914, p. 286. *Genotype* by original designation.—*Tenthredo luteiventris* Klug.

Tomostethus subg. *Atomostethus* Enslin, 1914, p. 287. *Genotype* by original designation.—*Tenthredo ephippium* Panzer. *New synonymy*.

Characteristics.—Differs from *Tethida* as follows: front wings with 2A & 3A represented only by a basal stub which may be curved up at the end, fig. 358; prepectus narrow, raised, and shoulder-like, fig. 362, set off by a deep furrow; tarsal claws simple; sheath narrow and blade-like.

Contains several species which appear to be truly holarctic.

Paracharactus MacGillivray

Paracharactus MacGillivray, 1908a, p. 292. *Genotype* by original designation.—*Paracharactus obscuratus* MacGillivray.

Characteristics.—Front wings with M usually parallel with 1m-cu but sometimes slightly divergent from it; stub of 2A & 3A straight at apex. Antennae narrow and slightly tapering, the segments of the flagellum decreasing almost imperceptibly in length. Malar space very narrow but distinct. Prepectal suture furrow-like, sometimes imperceptible. Tarsal claws simple or with a very small tooth. Sheath long, deep, thin and blade-like. Saw very simply serrate.

The few species in this genus have not yet been revised.

Claremontia Rohwer

Claremontia Rohwer, 1909, p. 397. Monobasic, *genotype*.—*Claremontia typica* Rohwer.

Differs from the above as follows: prepectus always absent. Tarsal claws with a longer tooth, fig. 357, and with the outer tooth more curved. Saw with lobiform teeth, resembling many species of *Blennocampa*.

Contains only the *genotype*.

Blennocampa Hartig

Blennocampa Hartig, 1837, p. 266. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo* (*Allantus*) *pusilla* Klug.

Monophadnus Hartig, 1837, p. 271. Genotype by subsequent designation of Ashmead, 1898.—*Tenthredo albipes* Gmelin. *New synonymy*.

Monophadnoides Ashmead, 1898, p. 253. Genotype by original designation.—*Monophadnus rubi* Harris. *New synonymy*.

Characteristics.—Front wing with stub of 2A & 3A straight, fig. 360. Antennae with third segment longer than fourth, fourth to ninth practically subequal, as in fig. 350. Malar space narrow to subobsolete, never wider than width of tibial spur. Prepectus absent. Tarsal claws and sheath various.

The nearctic species of this genus have never been revised. Probably a dozen valid species occur in this region.

Waldheimia Brullé

Waldheimia Brullé, 1846, p. 665. Genotype by original designation.—*Tenthredo braziliensis* Lepeletier.

Erythraspides Ashmead, 1898, p. 128. Genotype by original designation.—*Blennocampa pygmaea* Say. *New synonymy*.

Characteristics.—Differs from *Blennocampa* chiefly in the antennae, figs. 351, 352. The last four segments are reduced in length, usually together no longer than third; the fourth and fifth are longer and wider than the apical ones; the third is the longest and is wider at the apex. The species *carbonaria* (Cresson) differs from the others in having somewhat less differentiation among the antennal segments, but it is without doubt a generalized member of this genus.

Several species occur in the nearctic region but the largest representation of the genus occurs in the neotropical region.

Periclista Konow

Periclista Konow, 1886, p. 184, no. 2. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo* (*Allantus*) *lineolata* Klug.

Mogerus MacGillivray, 1895, p. 281. New name for *Periclista*.

Isodyctium Ashmead, 1898, p. 127. Genotype by original designation.—*Isodyctium caryiculum* Dyar.

Neocharactus MacGillivray, 1908a, p. 293. Monobasic, genotype.—*Neocharactus bakeri* MacGillivray. *New synonymy*.

Aphanisus MacGillivray, 1908a, p. 295. Genotype by original designation.—*Aphanisus lobatus* MacGillivray. *New synonymy*.

Apericlista Enslin, 1914, p. 265. Genotype by original designation.—*Tenthredo albipennis* Zaddach. *New synonymy*.

Characteristics.—Front wings with stub of 2A & 3A curved up at apex, fig. 358. Head with malar space wider than width of tibial spur, often as wide as length of second antennal segment; clypeus little de-

flected from head; frontal crest rounded off and not jutting forward, fig. 366. Antennae slightly tapering, fourth to ninth segments gradually decreasing in length, third usually longer than fourth. Prepectus absent. Tarsal claws with a medium-sized inner tooth. Males of many species with a peripheral vein as in fig. 180.

This is undoubtedly the largest Blennocampine genus in the nearctic region. The species whose biology is known feed on *Quercus* or *Hicoria*.

Pareophora Konow

Pareophora Konow, 1886, p. 184. Genotype by subsequent designation of Rohwer, 1911b.—*Pareophora luridiventris* Konow = *nigripes* (Klug).

Differs from the above chiefly in having simple tarsal claws. The head of our only species has long eyes with their inner margins parallel, fig. 368, and fairly short antennae.

Pareophora minuta (MacGillivray) new combination

Monophadnus minutus MacGillivray, 1908a, p. 291, ♀.

Pareophora guara MacGillivray, 1923a, p. 54, ♀. *New synonymy*.

Pareophora guana MacGillivray, 1923b, p. 29, ♀. *New synonymy*.

To date this is the only recorded nearctic species.

Valco new genus

Characteristics.—Front wings with stub of 2A & 3A curved up at apex, fig. 358. Prepectus absent. Malar space slightly wider than width of tibial spur. Clypeus projecting at a distinct angle from head, frontal crest also projecting prominently, and with postocellar furrows very deep and short. Antennae short, with third segment longer than fourth, fig. 350. Tarsal claws simple or with a small inner tooth.

Genotype by original designation.—*Selandria irrogata* Cresson.

This genus and several others, such as *Ardis*, *Pareophora*, *Eupareophora*, and *Monardis*, each contain only a few species and may need grouping together at a later date. Until more material is studied, however, there seems little choice but to draw the generic limits closely.

Lagonis new genus

Characteristics.—Front wings with stub of 2A & 3A curved up at apex, fig. 358. Head with wide malar space; eyes small, removed their own length from dorso-caudal margin, fig. 365. Antennae long and slender, third, fourth, and fifth segments subequal, sixth to ninth gradually decreasing in length, fig. 353. Prepectus absent. Scutellum and dorsal portion of mesepisternum with large, round punctures. Tarsal claws with a short inner tooth.

Genotype by original designation.—*Selandria nevadensis* Cresson.
Known only from the genotype.

Lagonis nevadensis (Cresson) new combination

Selandria nevadensis Cresson, 1880, p. 13, ♀.

Paracharactus leucostomus Rohwer, 1912b, p. 230, ♀. *New synonymy.*

The mesothorax of the female varies in color from almost totally rufous to totally black. The species is western in distribution.

Phymatocera Dahlbom

Phymatocera Dahlbom, 1835, p. 11. Monobasic, genotype.—*Tenthredo* (*Allantus*) *aterrima* Klug.

Pectinia Brullé, 1846, p. 664. Genotype by original designation.—*Tenthredo* (*Allantus*) *aterrima* Klug.

Melanoselandria Ashmead, 1899, p. 606. Monobasic, genotype.—*Melanoselandria zabriskiei* Ashmead. *New synonymy.*

Hypargyricus MacGillivray, 1908a, p. 290. Genotype by original designation.—*Hypargyricus infuscatus* MacGillivray. *New synonymy.*

Characteristics.—Front wings with stub of 2A & 3A furcate at apex, fig. 359. Malar space narrower than width of tibial spur. Antennae fairly filiform, usually with the fourth segment the longest, often with the apices of the segments considerably wider than the base. Prepectus present as a polished shoulder. Tarsal claws with a small inner tooth. Sheath blade-like, thin.

This genus contains five or six nearctic species which have never been revised. Most of them have the wings heavily and darkly infuscated.

Rhadinoceraea Konow

Rhadinoceraea Konow, 1886, p. 184. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo* (*Allantus*) *micans* Klug.

Differs from the above chiefly in lacking the prepectus. The tarsal claws may lack an inner tooth.

The few nearctic species resemble those of *Phymatocera* in appearance and also are in need of revision.

Ceratulus MacGillivray

Ceratulus MacGillivray, 1908c, p. 454. Genotype by original designation.—*Ceratulus spectabilis* MacGillivray.

Characteristics.—Front wing with stub of 2A & 3A straight, fig. 360. Antennae serrate, fig. 355, the lower, distal corner of the fourth to ninth segments markedly produced into a thumb-like process and the third segment triangular. Malar space about as long as width of tibial spur. Tarsal claws deeply cleft, the two rays subequal in size.

The genotype is the only species placed as yet in the genus, known only from Arizona.

SUBFAMILY LYCAOTINAE

Characteristics.—Prepectus absent. Cervical sclerites pointed and not approximate on meson. Front wings, fig. 192, with 2r present, M parallel with 1m-cu, 2A & 3A fused for a short distance with 1A, and the basal abscissa of 2A & 3A with only a poorly indicated sinuation, fig. 201. Hind wings with typical venation. Mandibles bidentate, fig. 46.

This is a small group which is undoubtedly the present day representative of the ancestor of the Tenthredininae. It contains two genera, separated basically by the radical differences in the female sex. Malaise (1933) has reunited these on the basis that genera are invalid if based only on characters confined to one sex or characters of an adaptive nature. This point of view seems to me untenable when one considers first the arbitrary nature of genera and secondly the difficulty encountered finding other diagnostic characters in many groups.

The characters of the members of this subfamily have been illustrated in detail by Ross (1932a).

KEY TO GENERA

1. Legs almost entirely black and wings entirely dark brown.....**Lycaota**
Legs light reddish brown and wings almost hyaline.....**Lycaotella**

Lycaota Konow

Lycaota Konow, 1903, p. 147. Monobasic, genotype.—*Selandria sodalis* Cresson.

Characteristics.—Hind tarsi shorter than middle tarsi but of same proportions, with a small tarsal claw with an exceedingly small tooth near middle, fig. 109. Tibial spurs of hind tarsi short, one-third length of tibia, fig. 109. Lancet of female saw with lobe-like teeth, fig. 363. Penis valve of male with circular head, fig. 371.

Contains only one species, the genotype.

Lycaotella Ross

Lycaotella Ross, 1932a, p. 41. Genotype by original designation.—*Selandria spissipes* Cresson.

Characteristics.—Similar in general to above. Differs as follows: female with front and middle tibiae and tarsi as for *Lycaota*, fig. 109, but with hind tibiae, fig. 111, thicker, evenly tapered and with tarsal segments short and stout, fig. 111, the tibial spurs three-fourths length of basitarsus and tarsal claw large with a long, pointed basal tooth giving the claw a chelate appearance. Female saw with serrate ventral margin, fig. 364. Male penis valve with rectangular head, fig. 372.

Contains only two species.

SUBFAMILY TENTHREDININAE

Characteristics.—Prepectus absent. Front wings, fig. 194, with M parallel with *lm-cu*, M joining R considerably basad of separation of R₁, and the sinuation of 2A & 3A almost smoothed out. Hind wings normal, sometimes with a peripheral vein in the male. Cervical sclerites, mandibles, and other characters various.

This subfamily represents one of the peaks of specialization in the Tenthredinidae. Within the subfamily can be traced a straight line development from the more primitive genera to the specialized. Apparently three characters have evolved hand in hand, the eyes, mandible, and cervical sclerites. Representative of the generalized condition is *Leucopelmonus*—mandibles bidentate, fig. 45, cervical sclerites pointed on meson, as in fig. 155, and eyes small, as in fig. 373. The specialized condition is found in *Tenthredo*—mandibles quadridentate, fig. 42, cervical sclerites truncate and appressed on meson as in fig. 158, and eyes usually large, fig. 375. Intermediates are furnished by *Zaschizonyx* and *Rhogogaster*.

The more primitive group is represented by several genera containing few species. They undoubtedly are remnants of evolutionary development, scattered widely over the holarctic region.

The recorded habits of the adults indicate that they are predaceous, which has probably paralleled the development of the specialized head.

KEY TO GENERA

1. Front wing with cell DA almost twice length of cell PA, fig. 380.....2
Front wing with cell DA less than one and one-half length of cell PA, fig. 381.....3
2. Inner margins of eyes straight and almost parallel, fig. 373.....**Lagium**
Inner margins of eyes distinctly converging below, fig. 375.....5
3. Sclerotized portion of basal plates forming a wide V on meson, nearly dividing the segment, fig. 379.....**Zaschizonyx**
Sclerotized portion of basal plates either completely contiguous on meson or forming a V no wider than in fig. 378.....4
4. Tarsal claws with inner tooth much shorter than outer one and well separated from it, fig. 389.....**Leucopelmonus**
Tarsal claws with inner tooth as long as the outer one and appressed to it, fig. 386.....5
5. Eyes seen from anterior aspect short and widely separated at base as in figs. 373, 374.....6
Eyes seen from anterior aspect larger and closer together at base as in fig. 375.....7
6. Clypeus with anterior margin straight or slightly sinuate, fig. 374.....**Aglaostigma**
Clypeus with anterior margin definitely emarginate, forming two lateral lobes, as in fig. 375.....**Rhogogaster**
7. Mandibles with two subapical teeth, the upper one sharp and the lower one truncate, fig. 382.....**Rhogogaster**

- Mandibles with more than two subapical teeth or not with the second one truncate, figs. 42, 43.....8
8. Middle coxae small, not overlapping the hind coxae, fig. 384.....**Macrophya**
Middle coxae larger, overlapping base of hind coxae, fig. 383.....9
9. Hind femora distinctly swollen in outline, fig. 385.....**Macrophya**
Hind femora slender, more nearly cylindrical, fig. 388.....**Tenthredo**

Leucopelmonus MacGillivray

Leucopelmonus MacGillivray, 1916, p. 83. Monobasic, genotype.—*Leucopelmonus annulatus* MacGillivray = *confusus* (Norton).

Characteristics.—Mandibles with only two teeth. Tarsal claws with inner tooth smaller than outer and separate from it, fig. 389. Clypeus deeply emarginate. Antennae long, slender, and setaceous. Eyes small and parallel, set far apart. Hind coxae not tremendously developed.

This genus is very closely related to the European *Perineura*, but differs in wing venation, mandibles, and genitalia.

Only a single species, the genotype, is known. Its synonymy has been given by MacGillivray (1919).

Lagium Konow

Lagium Konow, 1904, p. 246. Genotype by original designation.—*Tenthredo atroviolaceum* Norton.

Characteristics.—Mandibles with only two teeth. Tarsal claws with inner tooth same size as outer but not appressed to it. Clypeus shallowly but distinctly emarginate. Antennae long, slender, and setaceous. Eyes small and parallel, set far apart. Hind coxae large, appearing almost subequal in lateral area to mesoepisternum and sternum. The known species have the head, thorax, wings, and almost all the legs black.

There are five described species in the genus, but the status of some is open to question.

Aglaostigma Kirby

Aglaostigma Kirby, 1882, p. 325. Monobasic, genotype.—*Aglaostigma eburneiguttatum* Kirby.

Laurentia A. Costa, 1890, p. 173. Monobasic, genotype.—*Laurentia craverii* A. Costa = *Tenthredo gibbosa* Fallén. *New synonymy.*

Bivena MacGillivray, 1894, p. 328. Genotype by original designation.—*Bivena maria* MacGillivray = *Laurentia semilutea* (Norton). *New synonymy.*

Homoeoneura Ashmead, 1898, p. 313. Genotype by original designation.—*Pachyprotasis delta* Provancher = *Laurentia semilutea* (Norton). *New synonymy.*

Neopus Viereck in Smith, 1910, p. 585. Genotype by original designation.—*Tenthredo 14-punctata* Norton. *New synonymy.*

Macrophyopsis Enslin, 1913, p. 128. Genotype by original designation.—*Macrophya nebulosa* Ed. André. *New synonymy.*

Astochus MacGillivray, 1914a, p. 107. Genotype by original designation.—*Astochus fletcheri* MacGillivray = *Laurentia rubens* (Cresson).

Kincaidia MacGillivray, 1914b, p. 137. Genotype by original designation.—*Tenthredopsis ruficornis* MacGillivray.

Parallomma Malaise, 1933, p. 53. Genotype by original designation.—*Rhogogaster lichtwardti* Konow. *New synonymy*.

Neurosiobla Conde, 1935, p. 79. Genotype by original designation.—*Neurosiobla malaisei* Conde. *New synonymy*.

Characteristics.—Mandibles bidentate. Tarsal claws with inner tooth at least as stout and long as outer one, the two rays closely appressed, fig. 386. Antennae long and setaceous. Clypeus, fig. 374, with anterior margin straight or slightly sinuate. Eyes small, separated below by a distance greater than their height, their inner margins parallel or slightly converging below. Supraclypeal area raised and nodiform, pretentorinae large. Basal plates only partially fused on meson. Posterior coxae only moderately developed.

Seven species are represented in our fauna, involving considerable synonymy.

Zaschizonyx Ashmead

Zaschizonyx Ashmead, 1898, p. 257. Genotype by original designation.—*Hoplocampa montana* Cresson.

Opisthoneura Ashmead, 1898, p. 287. Genotype by original designation.—*Opisthoneura crevecoeuri* Ashmead = *Zaschizonyx montana* (Cresson).

Characteristics.—Mandibles with a third small tooth below apical pair, fig. 44. Tarsal claws as above. Labrum distinctly and angularly incised at apex. Clypeus deeply, circularly emarginate, the lateral angles sharp. Antennae short and filiform, the third segment considerably longer than the fourth. Head almost evenly convex, without deeply excavated furrows or high ridges. Eyes distant, distinctly converging below. Basal plates deeply excavated posteriorly on meson, fig. 379.

Contains only one species, the genotype.

Rhogogaster Konow

Rhogogaster Konow, 1884, p. 338. Genotype by subsequent designation of Rohwer, 1911b.—*Tenthredo viridis* Linnaeus.

Rhogogastera Konow, 1885b, p. 123. Emended name for *Rhogogaster*.

Characteristics.—Mandibles tridentate, the basal tooth on the right mandible small, on the left mandible large, fig. 382. Tarsal claws with appressed teeth. Antennae fairly long and setaceous. Labrum rounded, truncate, or slightly emarginate. Clypeus deeply emarginate. Supraclypeal area sloping up to form an angular crest between antennal sockets. Head shallow, eyes fairly distant and converging below, varying between the conditions shown in figs. 374, 375. Hind coxae not greatly developed. Basal plates various.

Contains four nearctic species, involving some synonymy.

Tenthredo Linnaeus

Tenthredo Linnaeus, 1758, p. 343. Genotype by subsequent designation of Latreille, 1810.—*Tenthredo scrophulariae* Linnaeus.

Labidia Provancher, 1886, p. 21. Monobasic, genotype.—*Labidia columbiana* Provancher = *opimus* Cresson.

Tenthredella Rohwer, 1910d, p. 117. Genotype by original designation.—*Tenthredo atra* Linnaeus.

Zamacrophya Rohwer, 1912b, p. 221. Genotype by original designation.—*Zamacrophya nigrilabris* Rohwer. *New synonymy*.

Characteristics.—Mandibles quadridentate, fig. 42, the apical tooth large, and simple, the next three more or less grouped together, the base sometimes projecting beneath this to form a tooth-like process. Eyes large and close together, fig. 375. Labrum usually slightly pointed, clypeus emarginate, antennae various. Head with deep furrows between eyes and antennae, and a crest between the antennal sockets. Tarsal claws with appressed teeth. Hind coxae only moderately developed.

This genus is one of the largest in the sawflies. Judging from present indications the genus has developed along many specialized lines in several parts of the world to form a large number of distinct phylogenetic units. Many of these units, however, are indicated only by male genitalia, and most can be separated only imperfectly by external characteristics. Many generic names have been applied to them but it seems best to reduce these to subgenera and thus remove unnecessary obstacles from the generic keys.

I believe that a satisfactory division of the genus into subgenera can be accomplished only after the world fauna is studied. Most of the nearctic species may be referred to one group with only few exceptions, so no effort is made here to subdivide the genus.

Macrophya Dahlbom

Macrophya Dahlbom, 1835, p. 11. Genotype by subsequent designation of Westwood, 1840.—*Tenthredo rusticus* auct., nec. Linnaeus = *Macrophya montana* Scopoli.

Pachyprotasis Hartig, 1837, p. 295. Genotype by subsequent designation of Westwood, 1840.—*Tenthredo rapae* Linnaeus.

Zalagium Rohwer, 1912b, p. 216. Genotype by original designation.—*Zalagium clypeatum* Rohwer. *New synonymy*.

Characteristics.—Mandibles quadridentate, forming more of a regularly decreasing series than in *Tenthredo*, fig. 43, the apical tooth largest. Eyes large and close together, fig. 375. Head without marked crest between or just above antennal sockets. Labrum usually truncate, clypeus variable. Tarsal claws with appressed teeth. Hind coxae large, appearing from lateral view nearly as large as mesosternum and episternum, and hind femora usually distinctly enlarged towards apex, fig. 385.

This genus contains a large nearctic fauna which is at present badly in need of revision.

SUPERFAMILY MEGALODONTOIDEA

FAMILY XYELIDAE

Diagnostic characters.—Antennae with the third segment elongate with a slender terminal filament composed of 9-25 segments, figs. 86, 87. Praescutum and scutellum distinct, scutum not divided transversely. Middle and hind tibiae with preapical spurs; front tibiae with two apical spurs, the longer one cleft at the apex, as in fig. 114. Front wings with vein R_4 divided, except in some species of *Xyela*.

Five genera are recognized in the nearctic fauna. They are markedly distinct from each other in many characters, including entirely different maxillae, clypei, wings, etc. This is another indication of the archaic nature of the family, for in no other group in the sawflies have the genera become so distinct morphologically.

The nearctic species have been discussed and keyed out by Ross (1932b) with the exception of the genus *Xyela* which was revised by Rohwer (1913).

KEY TO GENERA

1. Subcosta 2 either indistinguishable, fig. 392, or joining R before separation of R_4 , fig. 387.....2
 Subcosta 2 joining R_1 beyond separation of R_4 , fig. 393.....4
2. Media fused with R_4 very close to R, fig. 387.....**Xyelecia**
 Media either not fused with R_4 , fig. 172, or fused with it a considerable distance from R, fig. 390.....3
3. Antennae with apical thread as long as, or longer than, third segment, as in fig. 87.....**Xyela**
 Antennae with apical thread shorter than third segment, fig. 86....**Pleroneura**
4. Clypeus produced into an irregular pointed apex, fig. 398.....**Megaxyela**
 Clypeus produced into a regular, bilobate apex, fig. 395.....**Macroxyela**

Xyela Dalman

Pinicola Brebisson, 1818, p. 116, preoccupied. Genotype by subsequent designation of Rohwer, 1911b.—*Pinicola julii* Brebisson.

Xyela Dalman, 1819, p. 122. Genotype by subsequent designation of Curtis, 1824.—*Xyela pusilla* Dalman.

Tritokreion Schilling, 1825, p. 43. No included species.

Mastigocerus Klug, M. S., in Lepeletier, 1823. Reference unknown, a synonym of *Xyela* by Lepeletier (Rohwer, 1911).

Neoxyela Curran, 1923, p. 20. Monobasic, genotype.—*Neoxyela alberta* Curran. *New synonymy.*

Characteristics.—Antennal thread with nine segments, as long as, or longer than, third segment. Maxilla, fig. 61, with lacinia lobe-like; galea with an apical portion demarked by a crease, thus forming a distal "segment"; palpus with third segment very long, terminal thread mostly membranous and indistinctly divided into several segments. Front wings,

fig. 392, with subcosta either appressed to radial stem or distinct from it, with Sc_2 joining R before separation of R_1 ; so-called R_2 present or absent, cross-veins variable in number and position. Hind wings with cross-vein $2r-m$ absent. Female sheath either straight or curving downward, fig. 402.

The species of the genus are in need of a thorough revision based on enough specimens to give an accurate determination of variation in the characters now used in their classification.

The genus *Neoxyela* was erected by Curran for a species in which vein " R_2 " was atrophied, fig. 390. A series of specimens has shown that this is a variable character of no particular significance.

Pleroneura Konow

Pleroneura Konow, 1897a, p. 56. Genotype by subsequent designation of Rohwer, 1911b.—*Xyela dahli* Hartig.

Pleuroneura Ashmead, 1898, p. 214. Misspelling of *Pleroneura*.

Manoxyela Ashmead, 1898, p. 214. Genotype by original designation.—*Manoxyela californica* Ashmead.

Characteristics.—Antennae with terminal filament much shorter than third segment. Mouthparts and venation similar to *Xyela*. The front wing, fig. 172, is unique among sawflies in having R_1 and M entirely separate, with three cross-veins between them. Female sheath sabre-like, curving dorsad, fig. 403.

Seven nearctic species have been described in the genus but the status of most of them is not on a fundamental basis.

Xylecia Ross

Xylecia Ross, 1932b, p. 159. Monobasic, genotype.—*Xylecia nearctica* Ross.

Characteristics.—Antennae very long, fig. 87, antennal thread longer than third segment, composed of 24 or more segments. Maxillae as in fig. 62; lacinia knob-like; distagalia lobate and set with short, peg-like setae; palpus with third segment very long, terminal thread fused into a simple, elongate, submembranous segment, clothed with long setae. Front wings, fig. 387, with subcosta distinct and short, Sc_2 joining R before separation of R_1 , M joining R_1 close to radial stem. Hind wings with $2r-m$ atrophied. Female sheath very short and broad, fig. 391.

Contains only one species, the genotype.

Megaxyela Ashmead

Megaxyela Ashmead, 1898, p. 214. Genotype by original designation.—*Xyela major* Cresson.

Odontophyes Konow, 1899a, p. 42. Monobasic, genotype.—*Pleroneura avingrata* Dyar.

Paraxyela MacGillivray, 1912, p. 294. Genotype by original designation.—*Xyela tricolor* Cresson.

Characteristics.—Clypeus with a large, median, triangular tooth, fig. 398. Antennae with third segment three times as long as terminal filament, which has eight or nine segments. Maxillae as in fig. 65; lacinia spatulate; mesal lobe of galea short and broad; palpi with four segments, the last two subequal, the fourth sclerotized, with only weak setae, the apex membranous. Labial palpus with four segments. Front wings with subcosta distinct and long, Sc_2 joining R, beyond fork of R_1 . Hind wings with $2r-m$ present, fig. 176. Tarsal claws deeply cleft, the two rays subparallel.

Contains about five species.

Macroxyela Kirby

Macroxyela Kirby, 1882, p. 351. Genotype by original designation.—*Xyela ferruginea* Say.

Protoxyela MacGillivray, 1912, p. 294. Genotype by original designation.—*Xyela aenea* Norton.

Differs from the above as follows: clypeus, fig. 395, with two anterior lobes separated by a distinct emargination; labial palpi three segmented.

At present three species are placed in this genus, but the known differences between them are unsatisfactory and the species limits need further study.

FAMILY PAMPILIIDAE

Characteristics.—Antennae long, slender and multi-segmented, fig. 88. Head capsule, figs. 4, 5, with clypeus turned under and fused on venter with postgenae, labrum asymmetrical and carried on venter. Abdomen flattened, with sharp lateral margins. Remainder of body similar to Xyelidae. Wings with R_2 always absent.

This family is a close relative of the European family Megalodontidae, but differs in possessing a presternal bridge, vein Sc in the front wing and in lacking processes on the antennae of the male.

The nearctic species form a very uniform group. Very few characters have been discovered upon which to divide the group into definite segregates. The key characters listed below represent almost all those which seem to be definite and constant. These include the relative size of the tarsal claws, presence or absence of certain preapical spines on the tibiae, presence or absence of vein Sc_1 in the front wing and the shape of the seventh abdominal sternite in the female. Other characters, such as the post-genal ridge, relative length of the third antennal segment, and the junction of M with R or R_1 in the front wing, have been used to split off genera, but too many intermediate conditions arise for them to be employed for generic diagnosis. This arrangement of the genera is the same as that proposed by Rohwer in 1910b.

KEY TO GENERA

1. Anterior tibiae with a preapical spur, fig. 399.....**Acantholyda**
Anterior tibiae without a preapical spur.....2
2. Front wing with Sc_1 entirely or partially atrophied, figs. 396, 400.**Neurotoma**
Front wing with Sc_1 present, fig. 401.....3
3. Tarsal claws with a small tooth some distance below apex, fig. 404. **Cephalcia**
Tarsal claws with a large tooth near apex, which consequently appears bifid, fig. 405.....**Pamphilius**

Acantholyda A. Costa

Acantholyda A. Costa, 1894, p. 232. Genotype by subsequent designation of Rohwer, 1910b.—*Tenthredo erythrocephala* Linnaeus.

Itycorsia Konow, 1897d, p. 13. Genotype by subsequent designation of Rohwer, 1910b.—*Tenthredo hieroglyphica* Christ.

Characteristics.—Anterior tibiae with a preapical spur, fig. 399. Front wing with Sc_2 present. Tarsal claws with a small subapical tooth as in fig. 404. Female with seventh abdominal sternite divided on meson by a sub-triangular depression, fig. 409.

Contains a large number of nearctic species which have not been treated comprehensively. The group *Itycorsia* has been segregated on the basis of having a postgenal carina, but the character is not constant enough for accurate use.

Cephalcia Panzer

Cephalcia Panzer, 1805, Heft 86, pl. 9. Genotype by subsequent designation of Rohwer, 1911c.—*Cephalcia arvensis* Panzer = *Cephalcia signata* (Fabricius).

Cephaleia Jurine, 1807, p. 68. Genotype by subsequent designation of Rohwer, 1911c.—*Cephaleia arvensis* Panzer = *Cephalcia signata* (Fabricius).

Caenolyda Konow, 1897d, p. 15. Genotype by subsequent designation of Rohwer, 1910b.—*Tenthredo reticulata* Linnaeus.

Liolyda Ashmead, 1898, p. 209. Genotype by original designation.—*Lyda frontalis* Westwood.

Differs from *Acantholyda* in lacking the preapical spur on the front tibiae. Several nearctic species belong in the genus.

Neurotoma Konow

Neurotoma Konow, 1897d, p. 18. Genotype by subsequent designation of Rohwer, 1910b.—*Tenthredo flaviventris* Linnaeus.

Gongylocorsia Konow, 1897d, p. 19. Monobasic, genotype.—*Lyda mandibularis* Zaddach.

Characteristics.—Anterior tibiae without preapical spur. Front wings with Sc_1 partially or entirely atrophied, figs. 396, 400. Tarsal claws with a large inner tooth near apex. Female with seventh abdominal sternite incised on meson as in fig. 409.

Contains only two described nearctic species.

Pamphilius Latreille

Pamphilius Latreille, 1802, p. 303. Monobasic, genotype.—*Tenthredo sylvatica* Linnaeus.

Lyda Fabricius, 1804, p. 43. Genotype by subsequent designation of Curtis, 1831.—*Tenthredo sylvatica* Linnaeus.

Anoplolyda A. Costa, 1894, p. 233. Genotype by subsequent designation of Rohwer, 1910b.—*Lyda alternans* A. Costa.

Kelidoptera Konow, 1897d, p. 20. Monobasic, genotype.—*Lyda maculipennis* Stein.

Bactroceros Konow, 1897d, p. 21. Genotype by subsequent designation of Rohwer, 1910b.—*Tenthredo vaefer* Linnaeus.

Characteristics.—Anterior tibiae without preapical spur. Front wings with Sc_1 present. Tarsal claws with a large, inner tooth near apex, which appears cleft, fig. 405. Female with seventh abdominal sternite not incised but convex and slightly produced on meson, fig. 408.

A large number of species are contained in this genus. They have at various times been divided into smaller genera on the basis of M in the front wing joining R or R_s and whether or not the third antennal segment was subequal to or almost twice as long as the fourth. A study of many species shows that both of these characters intergrade from one extreme to the other, hence they cannot be used for definite dividing points.

SUPERFAMILY SIRICOIDEA

FAMILY SYNTECTIDAE

Diagnostic characters.—Antennae slender and setaceous, with about 16 segments, fig. 89. Tibiae without preapical spurs, front tibiae with only one apical spur which is pectinate on its inner margin, fig. 118. Mesonotum without a transverse suture, fig. 122.

This family contains only one described genus, *Syntexis* Rohwer, (1915c), with its sole species and genotype *S. libocedrii* Rohwer. It was placed by its describer in the family Cephidae, but differs from this family in having a genaponta instead of a maxaponta, in having cenchri and in lacking the distinct constriction between the first and second abdominal segments. *Syntexis* is most closely related to the Xiphydriidae, the two having similar antennae, wing venation, and type of head. *Syntexis* differs from the Xiphydriidae, however, in lacking the transverse suture of the mesoscutum, and in having a wide trench between the meso- and metanotum, fig. 122. On the basis of these characters Benson (1935b) erected a new family Syntexidae. According to the derivation of the name, however, the stem is *Syntect-*, and therefore the name should be Syntectidae.

The most distinctive characters of the genus are the incisions of the anterior margin of the mesoepisterna, fig. 130, and the curious formation

of the alaglossa of the labium, figs. 78, 79. These two conditions are found nowhere else in the sawflies and form the chief basis for considering the genus a separate family.

FAMILY XIPHYDRIIDAE

Diagnostic characters.—Antennae slender and setaceous, having about 20 segments, fig. 90. Tibiae without preapical spurs, front tibiae with only one apical spur, which is cleft at the apex, fig. 117. Mesoscutum with a transverse suture, fig. 123; mesosnotum and metanotum approximate, with none of the mesopostnotum visible. Head above the eyes rounded and dome-shaped, fig. 22.

The nearctic species represent only the typical genus.

Xiphydria Latreille

Xiphydria Latreille, 1802, p. 304. Monobasic, genotype.—*Ichneumon camelus* Linnaeus.

Hybonotus Klug, 1803, p. 8. Genotype by subsequent designation of Rohwer, 1911b. —*Ichneumon camelus* Linnaeus.

Xiphiura Fallén, 1813, p. 11. No species included.

Xiphidion Provancher, 1875, p. 374. Monobasic, genotype.—*Xiphidion canadense* Provancher = *Xiphydria mellipes* Harris.

Konowia Brauns, 1884, p. 220. Monobasic, genotype.—*Konowia megapolitana* Brauns. *New synonymy.*

Pseudoxiphydria Enslin, 1911, p. 177. Genotype by original designation.—*Pseudoxiphydria betulae* Enslin. *New synonymy.*

This genus contains several nearctic species which have been treated by Rohwer (1918a). Except for the wings, all the species have such a similar morphological pattern that it accomplishes nothing to divide them into more than one group. The venation of the front wing is somewhat variable, especially the proximity at their base of veins 1A and 2A & 3A and the completeness of cross-vein 3r-m, which may be complete, reduced to a stub, or absent. These are the characters upon which were based the genera *Konowia* and *Pseudoxiphydria*.

FAMILY SIRICIDAE

Diagnostic characters.—Antennae filiform, with about 15 segments, fig. 91, frequently bilaterally compressed. Tibiae without preapical spurs, front tibiae with only one apical spur which is cleft at the apex, fig. 116. Mesonotum with the praescutum indistinct, its sutures represented only by faint traces; the scutum with two diagonal furrows running from the lateral margin to the anterior margin of the scutellum, fig. 127.

Bradley (1913) has revised and keyed out the North American species and genera of this family.

KEY TO GENERA

1. Posterior tibiae with one apical spur.....2
 Posterior tibiae with two apical spurs.....3
2. Antennae filiform, with less than 18 segments.....4
 Antennae slender and tapering, with more than 20 segments.....*Xeris*
3. Head with a large white spot behind eye.....*Urocerus*
 Head without a white spot behind eye.....*Sirex*
4. Antennae with five segments.....*Terodon*
 Antennae with sixteen or more segments.....*Tremex*

SUBFAMILY SIRICINAE

Characterized chiefly by the labial palpi having three segments, fig. 84; presence of cerci; antennae with nineteen or more segments; and small cell 2R₁.

Sirex Linnaeus

Sirex Linnaeus, 1761, p. 396. Genotype by subsequent designation of Curtis, 1829.—

Sirex juvencus Linnaeus.

Pauturus Konow, 1896a, p. 41. Genotype by subsequent designation of Rohwer, 1911b.—*Sirex juvencus* Linnaeus.

Characteristics.—Head immaculate. Cornus of female more or less triangular, not constricted at base and widened at apex. Posterior tibiae with two apical spurs.

Contains seven or eight species.

Urocerus Geoffroy

Urocerus Geoffroy, 1762, p. 264. Monobasic, genotype.—*Ichneumon gigas* Linnaeus.

Differs from *Sirex* in having white marks behind the eyes, and in having a clavate cornus, which is constricted at the base.

There are four recognized species.

Xeris A. Costa

Xeris A. Costa, 1894, p. 295. Monobasic, genotype.—*Ichneumon spectrum* Linnaeus.

Differs from *Urocerus* in having the hind tibiae with only one apical spur and the ovipositor as long as the body.

Contains three species.

SUBFAMILY TREMICINAE

Characterized as follows: labial palpi with two segments; cerci absent; antennae with 17 segments or less; front wings with a long cell 2R₁.

The genus *Terodon* is known only from Cuba and is included in the key for convenience. Our only nearctic genus is *Tremex*.

Tremex Jurine

Tremex Jurine, 1807, p. 80. Genotype by subsequent designation of Latreille, 1810.—

Sirex fuscicornis Fabr.

Xyloterus Hartig, 1837, p. 385, preoccupied. Monobasic, genotype.—*Sirex fuscicornis* Fabricius.

Xyloecermatium L. Heyden, 1868, p. 227. New name for *Xyloterus*.

Characteristics as for subfamily. Contains only one nearctic species, *columba* (Linnaeus).

FAMILY ORUSSIDAE

Diagnostic characters.—Antennae with 10 segments, setaceous in the male, fusiform in the female, fig. 92, situated on the ventral aspect of the head, fig. 24. Tibiae without preapical spurs, front tibiae with two apical spurs, one very short, the other longer and cleft at the apex, fig. 115. Mesonotum with the praescutum more or less indistinct, the lateral sutures reaching the transverse suture of the scutum. Both wings with most of the venation represented only by pigmented bands, fig. 177.

KEY TO GENERA

1. Face with two sharp, high carinae, fig. 410.....**Ophrynopus**
 Face without high carinae.....2
2. Front wing with 2r joining stigma near apex, which is somewhat thickened, fig. 406.....**Ophrynella**
 Front wing with 2r joining stigma at middle, the apex of stigma gradually tapering to apex, fig. 407.....**Orussus**

Orussus Latreille

Orussus Latreille, 1796, p. 111. Genotype by subsequent designation of Latreille, 1810.—*Orussus coronatus* Fabricius = *O. abietinus* Scopoli.

Oryssus Fabricius, 1798, p. 218. Emended name for *Orussus* Latreille.

Characteristics.—Head with a crown of three pairs of distinct tubercles on dorsum, without carinae on face. Front wings with M joining R_s some distance from R; stigma tapering at apex, 2r joining it near middle, fig. 407. Hind femora more slender than in fig. 411.

Contains several nearctic species which have been treated by Rohwer (1912a).

Ophrynella new genus

Characteristics.—Head with a dorsal crown of five distinct pairs of tubercles forming a wide ring around anterior ocellus, as in fig. 23; front reticulate with close, sharp-walled pits but without carinae; postgenae with a distinct high crassa from mandible to dorsum of head. Maxillary palpi with five segments, the two basal ones short, the three apical ones long and slender. Front wings with stigma long, 2r joining it near apex, the apex slightly enlarged, fig. 406; base of R_s subequal to base of M. Hind femora swollen, fig. 411, the adjoining tibiae and tarsi short and stocky.

Genotype.—*Oryssus nigricans* Cameron (original designation and monobasic).

Benson (1936a) treats this species as a member of the genus *Ophrynopus*, but all described species of that genus have two high prominent

carinae with an anterior joining one on the front. The species *nigricans* is undoubtedly closely allied to *Ophrynopus* on the basis of wing venation but seems to form a distinct unit from it.

The genotype is the only species yet placed in the genus. It has recently been captured in Texas.

Ophrynopus Konow

Ophrynopus Konow, 1897c, p. 605. Genotype by subsequent designation of Rohwer, 1911b.—*Ophrynopus andrei* Konow.

Stirocorsia Konow, 1897b, p. 372. Monobasic, genotype.—*Stirocorsia kohli* Konow.

Differs from the above in having a series of high carinae on the front as in fig. 410.

To date only a single unidentified male of this genus has been recorded from the nearctic region, to wit, *Arizona*.

SUPERFAMILY CEPHOIDEA

FAMILY CEPHIDAE

(By Donald T. Ries, Ithaca, N. Y.)

Diagnostic characters.—Antennae with 20-30 segments, filiform, slightly fusiform, or clavate. Middle and hind tibiae frequently with preapical spurs; front tibiae with only one apical spur which is cleft at the apex, the inner tooth small and the outer tooth large, fig. 119. Cenchri absent, fig. 121. A distinct constriction between the first and second abdominal segments, fig. 143.

Detailed genitalic studies of the nearctic species together with a large number of the genotypes of many of the palearctic genera has shown that a large number of the genera must be grouped together in order to get a clear picture of the phylogeny of the Cephidae. This will result in some changes in the classification of the family as treated by Benson, 1935b. I have been unable to study sufficient species to make a complete classification of the world genera at the present moment but enough to make it possible to ascertain the limits of genera actually involved by nearctic species. For this reason only the generic names which involve nearctic species have been treated in this diagnosis.

In a revision of the nearctic Cephidae now nearing completion these phylogenetic groups will be taken up in greater detail.

KEY TO GENERA

1. Hind tibiae with preapical spurs, fig. 110.....2
Hind tibiae without preapical spurs.....**Caenocephus**
2. Tarsal claws with base wide and lobular below junction of teeth,
fig. 417.....**Janus**
Tarsal claws with base tapering and slender, fig. 420.....3

3. Flagellum constricted at base for less than one-fourth its length and with marked shortening of the segments occurring beyond the third, fig. 419.....**Hartigia**
 Flagellum constricted for half its length and with marked shortening of the segments not occurring until the fifth or sixth, figs. 416, 418.....**Cephus**

Caenocephus Konow

Caenocephus Konow, 1896b, p. 151. Monobasic, genotype.—*Caenocephus jakowleffi* Konow.

Characteristics.—Hind tibiae without preapical spurs. Antennae with third segment longer than fourth. Left mandible with two triangular subequal teeth of similar shape. Hind wings with *3r-m* absent. Tarsal claws with two stout, subequal apical teeth. Male sternites simple.

Contains only two described nearctic species from the Rocky Mountain region. These represent the two sexes of only one species.

Cephus Latreille

This genus embraces a large number of species which differ radically in the genitalia and ornamentation of the seventh to ninth abdominal sternites in the male. All other characters, however, group these species into a single phylogenetic unit, characterized by the shape of the tarsal claws and the antennae.

On the basis of the males it is possible to group the nearctic species into two subgenera as follows:

Eighth sternite at most with row of scale-like setae along apex, fig. 423 **Cephus**
 Seventh and eighth sternites with distinct cavities filled with long, needle-like setae, fig. 424.....**Trachelus**

Subgenus *Cephus* Latreille

Astutus Jurine, 1801, p. 163. Monobasic, genotype.—*Sirex pygmaeus* Linnaeus.

Name set aside by International Zoological Congress, 1935.

Cephus Latreille, 1802, p. 303. Genotype by subsequent designation of Latreille, 1810.—*Sirex pygmaeus* Linnaeus.

Calameuta Konow, 1896b, p. 159. Genotype by subsequent designation of Rohwer, 1911b.—*Cephus filiformis* Eversmann. *New synonymy*.

Characteristics.—Hind tibiae with one or two preapical spurs. Hind wings with *3r-m* present. Tarsal claws various, figs. 421, 422. Antennae slightly clavate beyond tenth segment.

Contains three species in the nearctic region, including the western grain-stem sawfly, *C. cinctus* Norton, and the European wheat-stem sawfly, *C. pygmaeus* (Linnaeus).

Subgenus *Trachelus* Fabricius

Astutus Panzer, 1801, p. 83, preoccupied. Genotype by subsequent designation of Rohwer, 1911b.—*Sirex troglodyta* Fabricius.

Trachelus Jurine, 1807, p. 70. Monobasic, genotype.—*Sirex tabidus* Fabricius.

Cepha Billberg, 1820, p. 98. Monobasic, genotype.—*Sirex tabida* Fabricius.

Eumetabolus Shulz, 1906, p. 211. New name for *Astatus* Panzer.

Trachelastatus Morice and Durrant, 1915, p. 383. New name for *Cepha* Billberg.

Our fauna contains only the introduced black wheat-stem sawfly, *C. tabidus* (Fabricius).

Janus Stephens

Janus Stephens, 1835, p. 107. Genotype by subsequent designation of Westwood, 1840.—*Janus connectens* Stephens = *Janus luteipes* (Lepeletier).

Phyllocus Newman, 1838, p. 485. Monobasic, genotype.—*Phyllocus faunus* Newman.

Ephippionotus O. Costa, 1860, p. 10. Monobasic, genotype.—*Ephippionotus luteiventris* O. Costa = *Janus compressus* (Fabricius).

Characteristics.—Antennae with flagellum narrow at base (first three segments), remainder uniformly wider with the exception of a slight tapering towards apex, fig. 419. Left mandible bidentate, the upper tooth shouldered at base, fig. 415. Tarsal claws with extremely wide base which appears as a broad basal tooth; the two apical teeth long, stout, and curved at a distinct angle to the base, fig. 417. Male abdomen without ornamentation on the sternites. Some species (*Janus abbreviatus* and male of *J. bimaculatus*) exhibit an interesting condition of a partial atrophy of cross-vein *lr*.

Contains four nearctic species, two of which have been reared from willow, poplar, and currant.

Hartigia Schiödte

Hartigia Schiödte, 1838, p. 332. Genotype by subsequent designation of Boie, 1855.—*Astatus satyrus* Panzer = *Hartigia nigra* (Harris).

Cerobactrus O. Costa, 1859, p. 9. Monobasic, genotype.—*Macrocephus ulmariae* Schlectendal = *Hartigia linearis* (Schränk).

Cephosoma Grادل, 1881, p. 294. Monobasic, genotype.—*Cephosoma syringae* Grادل = *Hartigia nigra* (Harris).

Copiosoma Kirby, 1882, p. 364. Misspelling for *Cephosoma* Grادل.

Adirus Konow, 1899b, p. 74. Monobasic, genotype.—*Cephus trimaculatus* Say.

Paradirus Dönnar-Zapolskij, 1931, p. 39. Monobasic, genotype.—*Paradirus algericus* Dönnar-Zapolskij.

Characteristics.—Antennae with flagellum narrow at base (first three segments), remainder fairly stout, slightly and evenly fusiform, fig. 419. Left mandible bidentate, the upper tooth with a wide base and a small nipple-like apex, fig. 414. Tarsal claws slender, with large inner tooth, both teeth curving considerably from axis of claw, fig. 420. Male abdominal sternites simple.

Contains three described species from the nearctic region of which *H. cressoni* (Kirby) mines in the stems of raspberries, blackberries, and roses, and *H. trimaculatus* (Say) bores in blackberries and roses.

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PLATES

Unless otherwise noted, all figures represent parts of adult insects.

PLATE I.

- FIG. 1.—Head of *Tenthredo basilaris* Say, anterior aspect.
 FIG. 2.—Head of *Tenthredo basilaris*, posterior aspect.
 FIG. 3.—Tentorium of *Macroxyela ferruginea* (Say), lateral aspect.
 FIG. 4.—Head of *Acantholyda luteomaculata* (Cress.), anterior aspect.
 FIG. 5.—Head of *Acantholyda luteomaculata*, posterior aspect.
 FIG. 6.—Tentorium of *Tenthredo basilaris*, lateral aspect.
 FIG. 7.—Head of *Cephus cinctus* Nort., anterior aspect.
 FIG. 8.—Head of *Cephus cinctus*, posterior aspect.
 FIG. 9.—Tentorium of *Cimbex americana* Leach, lateral aspect.
 FIG. 10.—Head of *Aleiodes terminalis* (Cress.), anterior aspect.
 FIG. 11.—Head of *Aleiodes terminalis*, posterior aspect.
 FIG. 12.—Tentorium of *Janus integer* (Nort.), lateral aspect.
 FIG. 13.—Labrum of *Lycaotella spissipes* (Cress.).
 FIG. 14.—Labrum of *Acantholyda luteomaculata*.
 FIG. 15.—Labrum of *Orussus terminalis* Newm.
 FIG. 16.—Labrum of *Tremex columba* (L.).
 FIG. 17.—Tentorium of *Aleiodes terminalis*, lateral aspect.

Abbreviations

<i>cl</i> clypeus	<i>l</i> labrum	<i>pg</i> postgena
<i>cp</i> corpotentorium	<i>m</i> mandible	<i>pr</i> pretentorium
<i>cpt</i> corpotendon	<i>mp</i> maxaponta	<i>pta</i> pretentorina
<i>cr</i> crassa	<i>mt</i> metatentorium	<i>ptc</i> postcoila
<i>e</i> compound eye	<i>mtr</i> metatentorina	<i>st</i> supratentorium
<i>ep</i> epicranial stem	<i>mx</i> maxillaria	<i>sta</i> supratentorina
<i>f</i> frontal region	<i>o</i> ocelli	<i>tt</i> course of tentorial
<i>fcl</i> fronto-clypeal	<i>oc</i> occipital region	thickenings
suture	<i>ocul</i> ocularium	
<i>g</i> gena	<i>od</i> odontoidea	

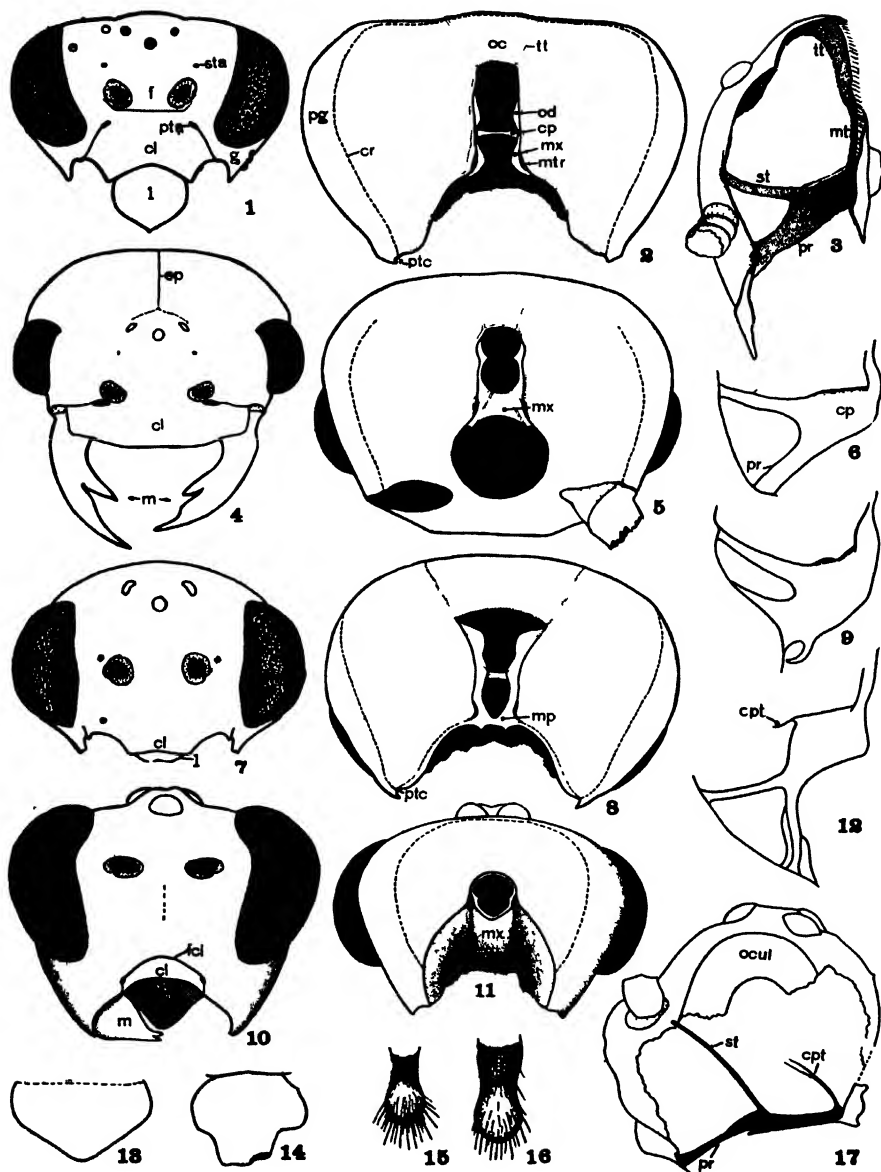


PLATE I

PLATE II

- FIG. 18.—Head of *Tremex columba*, anterior aspect.
 FIG. 19.—Head of *Tremex columba*, posterior aspect.
 FIG. 20.—Head of *Syntexis libocedrii* Rohwer, left half anterior aspect, right half posterior aspect.
 FIG. 21.—Head of *Syntexis libocedrii*, lateral aspect.
 FIG. 22.—Head of *Xiphydria maculata* Say, lateral aspect.
 FIG. 23.—Head of *Orussus terminalis*, left half anterior aspect, right half posterior aspect.
 FIG. 24.—Head of *Orussus terminalis*, ventral aspect.
 FIG. 25.—Head of *Xiphydria maculata*, lateral portion cut away to show tentorium.
 FIG. 26.—Tentorium of *Orussus terminalis*, lateral aspect.
 FIG. 27.—Tentorium of *Orussus terminalis*, dorsal aspect.
 FIG. 28.—Tentorium of *Aleiodes terminalis*, dorsal aspect.
 FIG. 29.—Tentorium of *Macroxyela ferruginea*, dorsal aspect.
 FIG. 30.—Tentorium of *Tremex columba*, lateral aspect.
 FIG. 31.—Tentorium of *Tremex columba*, dorsal aspect.
 FIG. 32.—Left mandible of *Xiphydria maculata*.
 FIG. 33.—Left mandible of *Syntexis libocedrii*.
 FIG. 34.—Mandibles of larva of *Sterictiphora apios* Ross, ventral aspect.
 FIG. 35.—Mandibles of *Macroxyela ferruginea*, dorsal aspect.
 FIG. 36.—Mandibles of *Janus integer*, dorsal aspect.
 FIG. 37.—Right mandible of *Orussus terminalis*, lateral and dorsal aspects, respectively.
 FIG. 38.—Mandibles of *Sterictiphora apios*, dorsal aspect.

Abbreviations

<i>cl</i> clypeus	<i>gr</i> antennal groove	<i>pr</i> pretentorium
<i>cp</i> corpotentorium	<i>l</i> labrum	<i>pta</i> pretentorina
<i>cpt</i> corpotendon	<i>m</i> mandibles	<i>px</i> proxadentes
<i>da</i> distadentes	<i>mo</i> mola	<i>st</i> supratentorium
<i>f</i> frontal region	<i>mx</i> maxillaria	<i>sta</i> supratentorina
<i>g</i> gena	<i>od</i> odontoidea	<i>tt</i> course of tentorial
<i>gp</i> genaponta	<i>pg</i> postgenae	thickenings

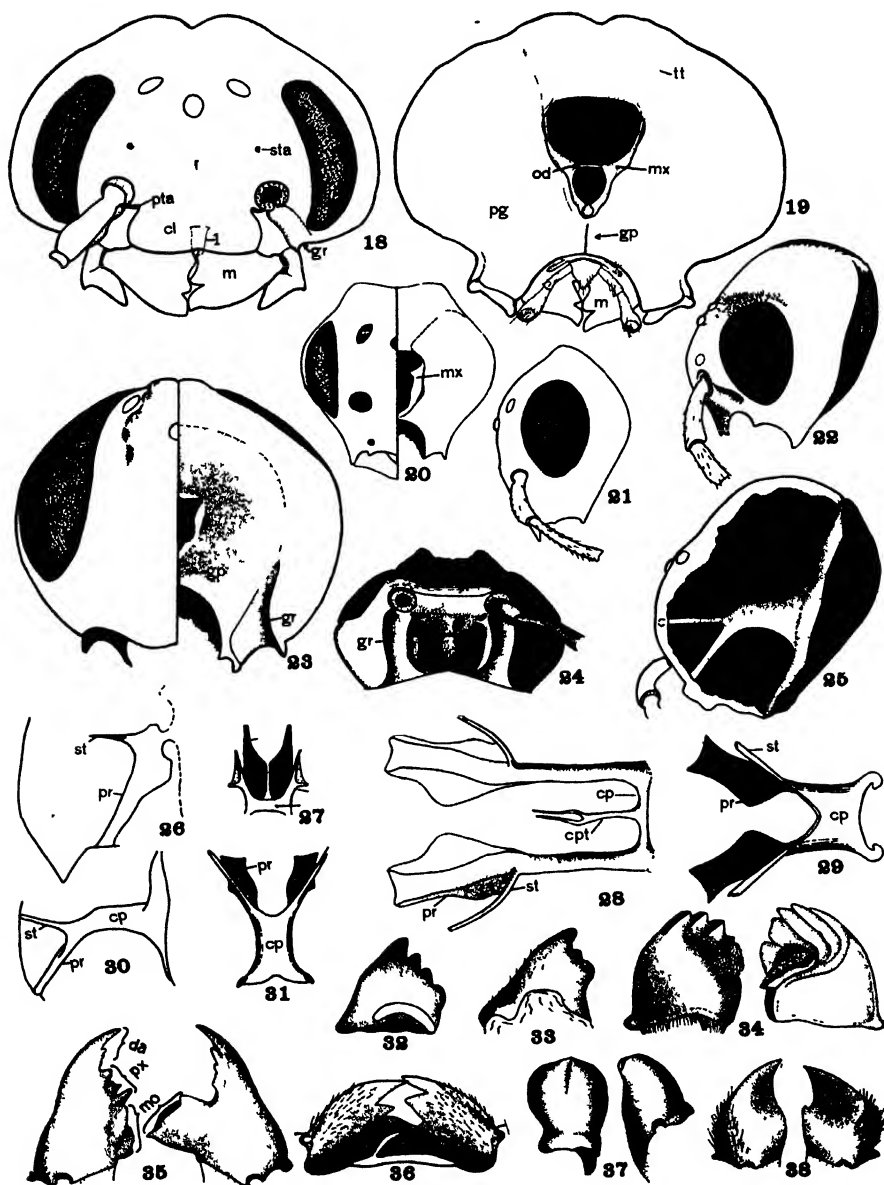


PLATE II

PLATE III

MANDIBLES, ANTERIOR ASPECT

- FIG. 39.—Right mandible of *Phymatocera fumipennis* (Nort.).
FIG. 40.—Right mandible of *Tethida cordigera* (Beauv.).
FIG. 41.—Right mandible of *Tomostethus multicinctus* Rohwer.
FIG. 42.—Right mandible of *Tenthredo mellicoxa* Prov.
FIG. 43.—Right mandible of *Macrophya rapae* (L.).
FIG. 44.—Right mandible of *Zaschizonyx montana* (Cress.).
FIG. 45.—Right mandible of *Aglaostigma rubens* (Cress.).
FIG. 46.—Right mandible of *Lycaotella spissipes*.
FIG. 47.—Left mandible of *Taxonus pallidicornis* (Nort.).
FIG. 48.—Right mandible of *Eriocampa rotunda* (Nort.).
FIG. 49.—Mandibles of *Taxonus epicera* Say.
FIG. 50.—Mandibles of *Allantus cinctus* (L.).
FIG. 51.—Right mandible of *Strongylogaster distans* Nort.
FIG. 52.—Right mandible of *Dolerus acidus* MacG.
FIG. 53.—Right mandible of *Caliroa cerasi* (L.).
FIG. 54.—Right mandible of *Phyllotoma nemorata* (Fall.).
FIG. 55.—Right mandible of *Fenusa dohrnii* (Tischb.).
FIG. 56.—Right mandible of *Cladius isomerus* Nort.
FIG. 57.—Right mandible of *Hoplocampa* sp.
FIG. 58.—Left mandible of *Hemichroa militaris* (Cress.).
FIG. 59.—Mandibles of *Nematus mendicus* Walsh.
FIG. 60.—Left mandible of *Euura salicis-nodus* Walsh.

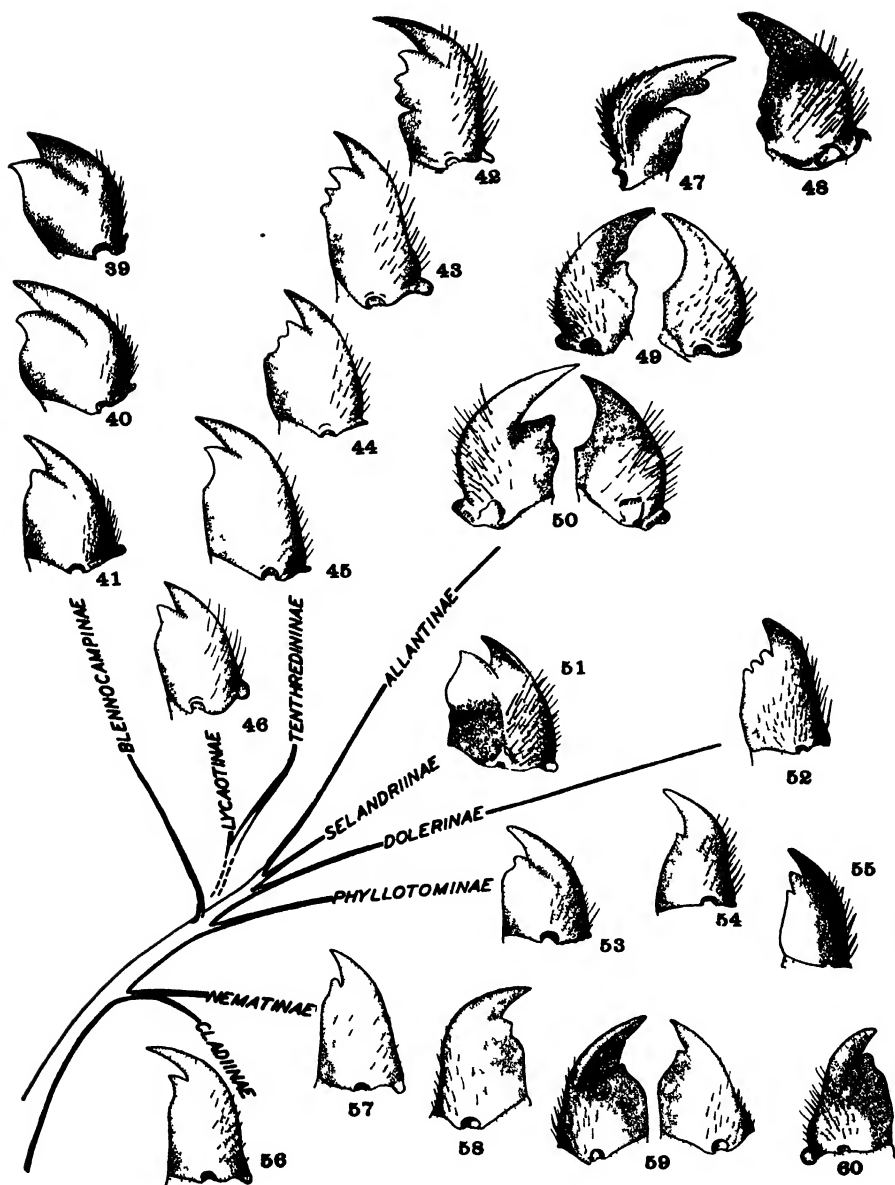


PLATE III

PLATE IV

MAXILLAE, POSTERIOR ASPECT

- FIG. 61.—Galea and lacinia of *Pleroneura aldrichi* Ross.
FIG. 62.—Galea and lacinia of *Xyelecia nearctica* Ross.
FIG. 63.—*Arge pectoralis* (Leach).
FIG. 64.—*Trichiosoma triangulum* Kirby.
FIG. 65.—*Macroxyela ferruginea*.
FIG. 66.—*Cephus cinctus*.
FIG. 67.—*Aleiodes terminalis*.
FIG. 68.—*Orussus terminalis*.
FIG. 69.—*Xiphydria maculata*.
FIG. 70.—*Syntexis libocedrii*.

Abbreviations

cd cardo
ecg ectogalea
eg endogalea

eus eustipes
gl galea
lc lacinia

p palpus
ps parastipes

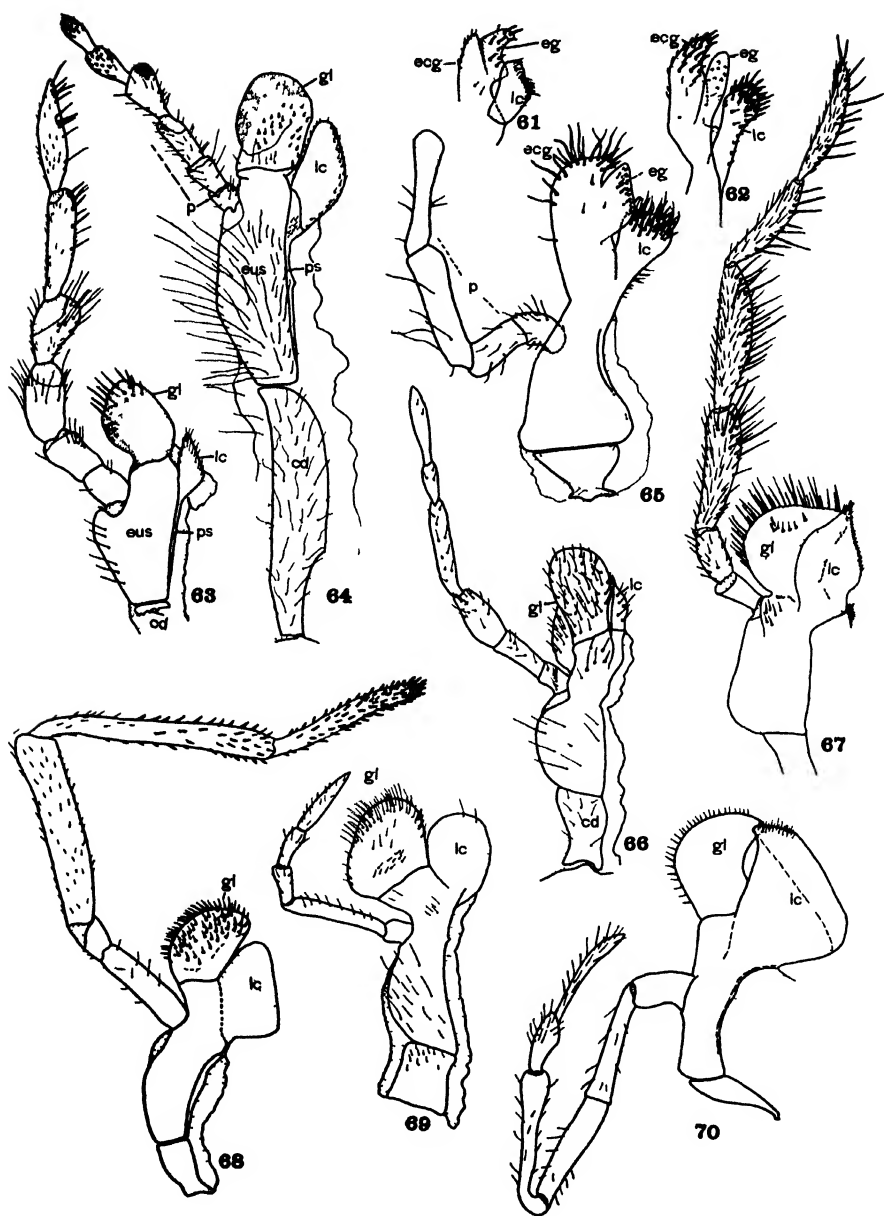


PLATE IV

PLATE V

- FIG. 71.—Labium of *Trichiosoma triangulum*, posterior aspect.
 FIG. 72.—Labium of *Arge pectoralis*, lateral aspect.
 FIG. 73.—Submentum and stipulae of *Arge pectoralis*.
 FIG. 74.—Labium of *Aleiodes terminalis*, posterior aspect.
 FIG. 75.—Labium of *Aleiodes terminalis*, lateral aspect.
 FIG. 76.—Totaglossa of *Incalia hirticornis* Cam., posterior aspect.
 FIG. 77.—Labium of *Macroxyela ferruginea*, posterior aspect.
 FIG. 78.—Labium of *Syntexis libocedrii*, posterior aspect.
 FIG. 79.—Labium of *Syntexis libocedrii*, lateral aspect.
 FIG. 80.—Labium of *Orussus terminalis*, posterior aspect.
 FIG. 81.—Labium of *Janus integer*, posterior aspect.
 FIG. 82.—Labium of *Xiphydria maculata*, posterior aspect.
 FIG. 83.—Paraglossae and alaglossa of *Xiphydria maculata*.
 FIG. 84.—Maxillae and labium of *Urocerus flavicornis* Fab., dorsal aspect.
 FIG. 85.—Labium of *Urocerus flavicornis*, lateral aspect.

Abbreviations

<i>alg</i> alaglossa	<i>max.p</i> maxillary palpus	<i>st</i> stipites
<i>cd</i> cardo	<i>p</i> labial palpus	<i>sti</i> stipulae
<i>dgl</i> duplaglossa	<i>pgl</i> paraglossa	<i>tgl</i> totaglossa
<i>gl</i> galea	<i>sm</i> submentum	<i>x</i> sclerotized area
<i>hy</i> hypopharynx		

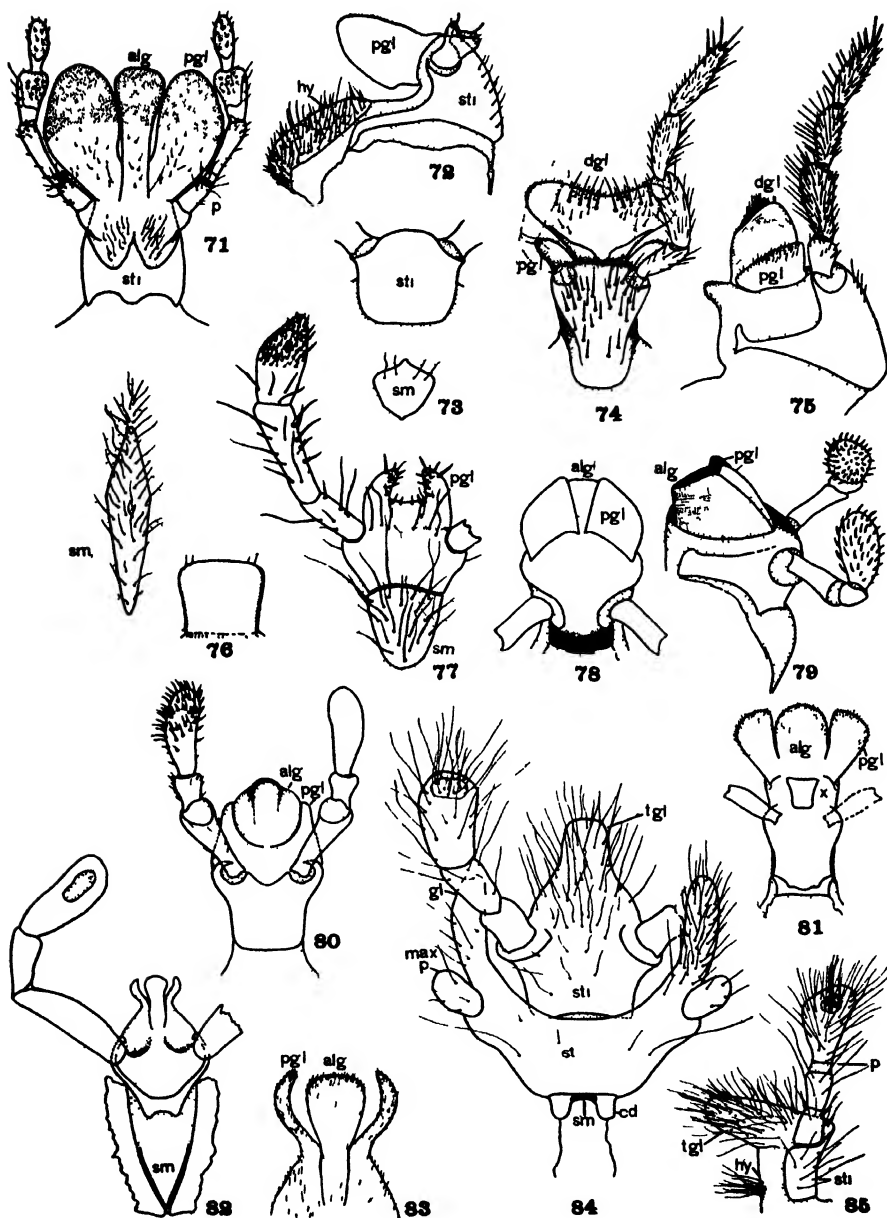


PLATE V

PLATE VI

- FIG. 86.—Antenna of female *Pleroneura aldrichi*.
 FIG. 87.—Antenna of female *Xylecia nearctica*.
 FIG. 88.—Antenna of female *Acantholyda luteomaculata*.
 FIG. 89.—Antenna of female *Syntexis libocedrii*.
 FIG. 90.—Antenna of female *Xiphydria maculata*.
 FIG. 91.—Antenna of female *Tremex columba*.
 FIG. 92.—Antenna of female *Orussus terminalis*.
 FIG. 93.—Antenna of female *Hemitaxonus dubitatus* (Nort.).
 FIG. 94.—Antenna of male *Megalodonta* sp.
 FIG. 95.—Antenna of female *Acordulecera* sp.
 FIG. 96.—Antenna of female *Blasticotoma filiceti* (Klug).
 FIG. 97.—Antenna of female *Sterictiphora zabriskiei* (W. & M.).
 FIG. 98.—Antenna of male *Sterictiphora cellularis* (Say).
 FIG. 99.—Antenna of female *Zaraea americana* (Cress.).
 FIG. 100.—Antenna of female *Trichiosoma triangulum*.
 FIG. 101.—Antenna of female *Tenthredo subnigriceps* Rohwer.
 FIG. 102.—Antenna of female *Tenthredo originalis* Norton.
 FIG. 103.—Antenna of female *Macrophya montana* (Scopoli).
 FIG. 104.—Antenna of male *Cladius isomerus*.
 FIG. 105.—Antenna of male *Monoctenus* sp.
 FIG. 106.—Antenna of female *Neodiprion affinis* Rohwer.
 FIG. 107.—Antenna of female *Augomonoctenus libocedrii* Rohwer.
 FIG. 108.—Front leg of female *Orussus terminalis*.
 FIG. 109.—Hind tarsi of female *Lycaota sodalis* (Cress.).
 FIG. 110.—Hind leg of *Janus integer*.
 FIG. 111.—Hind tarsi of female *Lycaotella spissipes*.
 FIG. 112.—Hind tibiae and tarsi of *Xiphydria maculata*.
 FIG. 113.—Apex of front tibia, tibial spurs and basitarsus of *Neodiprion affinis*.
 FIG. 114.—Apical spurs of front tibia of *Lycaota sodalis*.
 FIG. 115.—Apical spurs of front tibia of *Orussus terminalis*.
 FIG. 116.—Apical spur of front tibia of *Tremex columba*.
 FIG. 117.—Apical spur of front tibia of *Xiphydria maculata*.
 FIG. 118.—Apical spur of front tibia of *Syntexis libocedrii*.
 FIG. 119.—Apical spur of front tibia of *Janus integer*.

Abbreviations

asp apical spurs
cx coxa
fm femur

psp preapical spurs
ta tarsi
tb tibia

tc tarsal claws
tr trochanters

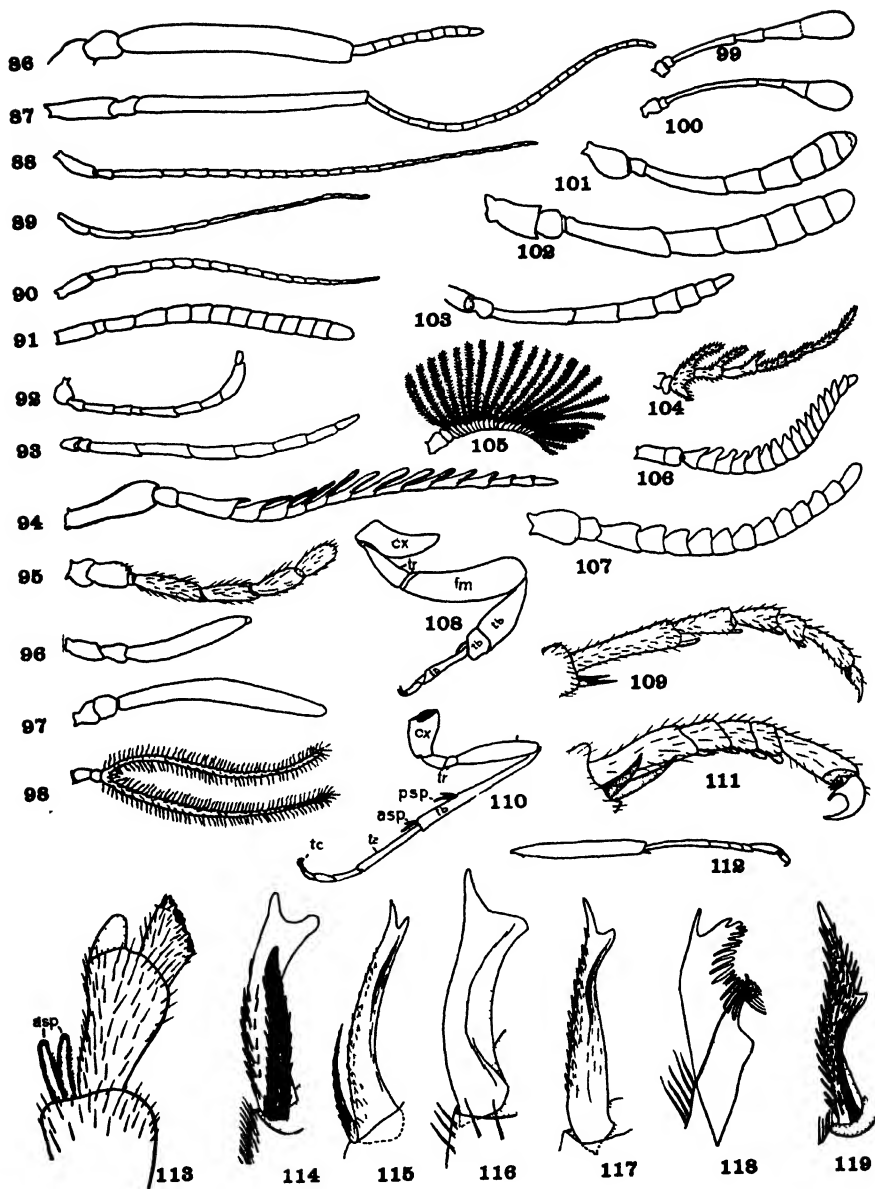


PLATE VI

PLATE VII

- FIG. 120.—Thorax of *Macroxyela ferruginea*, dorsal aspect.
 FIG. 121.—Thorax of *Janus integer*, dorsal aspect.
 FIG. 122.—Thorax of *Syntexis libocedrii*, dorsal aspect.
 FIG. 123.—Thorax of *Xiphydria maculata*, dorsal aspect.
 FIG. 124.—Pro- and mesonotum of *Profenusa canadensis* (Marl.).
 FIG. 125.—Post-tergite of *Dolerus similis* (Norton).
 FIG. 126.—Pro- and mesonotum of *Acordulecera* sp.
 FIG. 127.—Pro- and mesonotum of *Tremex columba*.
 FIG. 128.—Thorax of *Orussus terminalis*, dorsal aspect.
 FIG. 129.—Thorax of *Macroxyela ferruginea*, ventral aspect.
 FIG. 130.—Thorax of *Syntexis libocedrii*, ventral aspect.
 FIG. 131.—Thorax of *Janus integer*, ventral aspect.
 FIG. 132.—Thorax of *Xiphydria maculata*, ventral aspect.
 FIG. 133.—Thorax of *Orussus terminalis*, ventral aspect.
 FIG. 134.—Mesothorax of *Arge pectoralis*, ventral aspect.
 FIG. 135.—Mesothorax of *Hemitaxonus dubitatus*, ventral aspect.
 FIG. 136.—Portion of mesothorax of *Allantus cinctus*, ventral aspect.
 FIG. 137.—Anterior portion of mesosternum of *Tremex columba*, ental aspect.
 FIG. 138.—Mesothorax of *Tremex columba*, ventral aspect.

Abbreviations

<i>ax</i> axillary sclerites	<i>pp</i> prepectus	<i>y</i> lobes of meso-
<i>bs</i> basisternum	<i>prs</i> praescutum	scutum
<i>cn</i> cenchri	<i>psb</i> presternal bridge	<i>1, 2</i> first and second
<i>cv</i> cervical sclerites	<i>pt</i> post-tergite	segments of
<i>eps</i> episternum	<i>ptn</i> postnotum	abdomen
<i>is</i> parascutellum	<i>scl</i> scutellum	<i>I, II, III</i> first, second, and
<i>ms</i> mesosternum	<i>scut</i> scutum	third segments
<i>pn</i> pronotum	<i>ss</i> spinisternum	of thorax

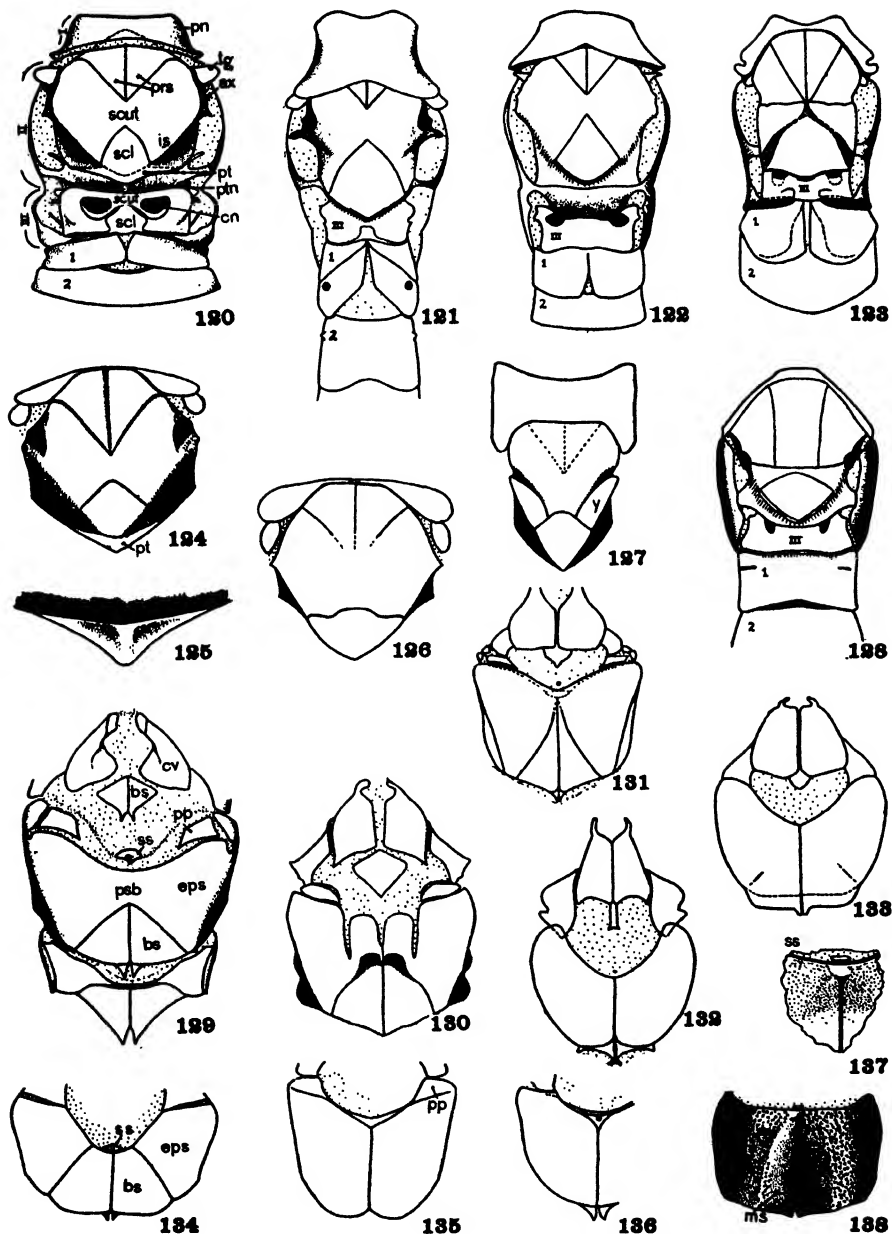


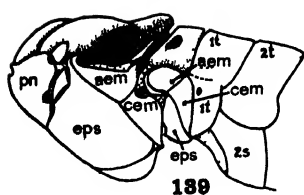
PLATE VII

PLATE VIII

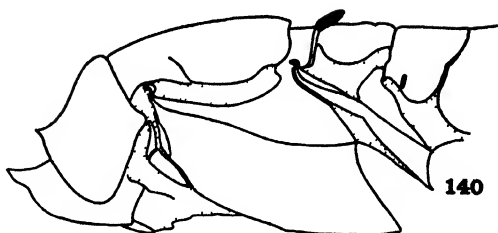
- FIG. 139.—Thorax of *Arge pectoralis*, lateral aspect.
 FIG. 140.—Thorax of *Syntexis libocedrii*, lateral aspect.
 FIG. 141.—Thorax of *Xiphydria maculata*, lateral aspect.
 FIG. 142.—Thorax of *Orussus terminalis*, lateral aspect.
 FIG. 143.—Thorax of *Janus integer*, lateral aspect.
 FIG. 144.—Thorax of *Eremotylus* sp., lateral aspect.
 FIG. 145.—Cervicum and propleurae of *Panorpa sigmoides* Carpenter, lateral aspect.
 FIG. 146.—Cervicum and propleurae of *Arge pectoralis*, lateral aspect.
 FIG. 147.—Cervicum and propleurae of *Xiphydria maculata*, lateral aspect.
 FIG. 148.—Cervicum and propleurae of *Macroxyela ferruginea*, lateral aspect.
 FIG. 149.—Postnotum of *Macroxyela ferruginea*.
 FIG. 150.—Postnotum of *Orussus terminalis*.
 FIG. 151.—Postnotum of *Tremex columba*.
 FIG. 152.—Postnotum of *Janus integer*.
 FIG. 153.—Profurcella and mesofurcella of *Acantholyda* sp.
 FIG. 154.—Cervicum and probasisternum of *Macrophya formosa* Klug.
 FIG. 155.—Cervicum and probasisternum of *Strongylogaster distans*.
 FIG. 156.—Cervicum and probasisternum of *Hemitaxonus dubitatus*.
 FIG. 157.—Cervicum and probasisternum of *Eriocampa rotunda*.
 FIG. 158.—Cervicum and probasisternum of *Allantus cinctus*.
 FIG. 159.—Cervicum and probasisternum of *Zaraea americana*.

Abbreviations

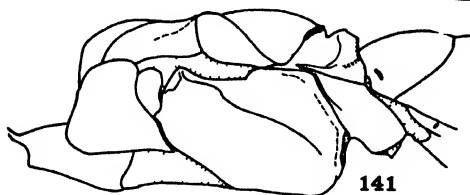
<i>aem</i> anepimeron	<i>f</i> furcella of prospini-	<i>1t</i> } tergites of first and
<i>cem</i> katapimeron	sternum	<i>2t</i> } second abdominal
<i>cv</i> cervical sclerites	<i>pl</i> propleurae	segments
<i>eps</i> episternum	<i>pn</i> pronotum	
<i>fc</i> furca of mesobasi-	<i>2s</i> sternite of second	
sternum	abdominal segment	



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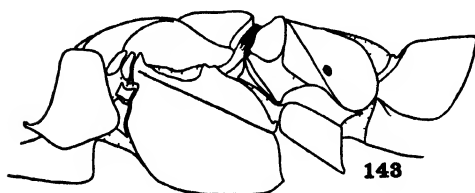
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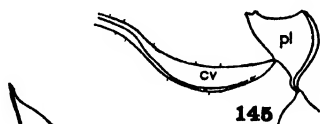
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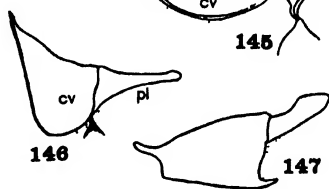
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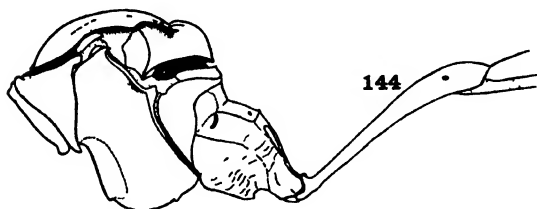


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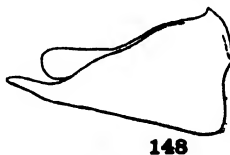


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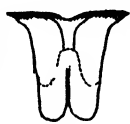
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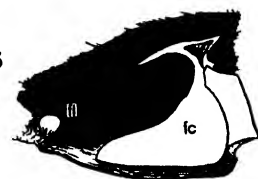
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PLATE IX

MALE GENITALIA, figs. 160 and 162-169, with dorsal aspect on left half and ventral aspect on right

- FIG. 160.—*Arge pectoralis*.
FIG. 161.—Sagittae and volsellae of *Xiphydria maculata*.
FIG. 162.—*Xiphydria maculata*.
FIG. 163.—*Trichiosoma triangulum*.
FIG. 164.—*Acordulecera* sp.
FIG. 165.—*Janus integer*.
FIG. 166.—*Urocerus flavicornis*.
FIG. 167.—*Macroxyela ferruginea*.
FIG. 168.—*Aleiodes terminalis*.
FIG. 169.—*Orussus terminalis*.

Abbreviations

<i>ca</i> gonocardo	<i>go</i> gonostipes	<i>py</i> penis valvae
<i>gg</i> parapenis	<i>h</i> harpes	<i>sa</i> sagittae
<i>gm</i> gonamaculae	<i>ol</i> volsellae	

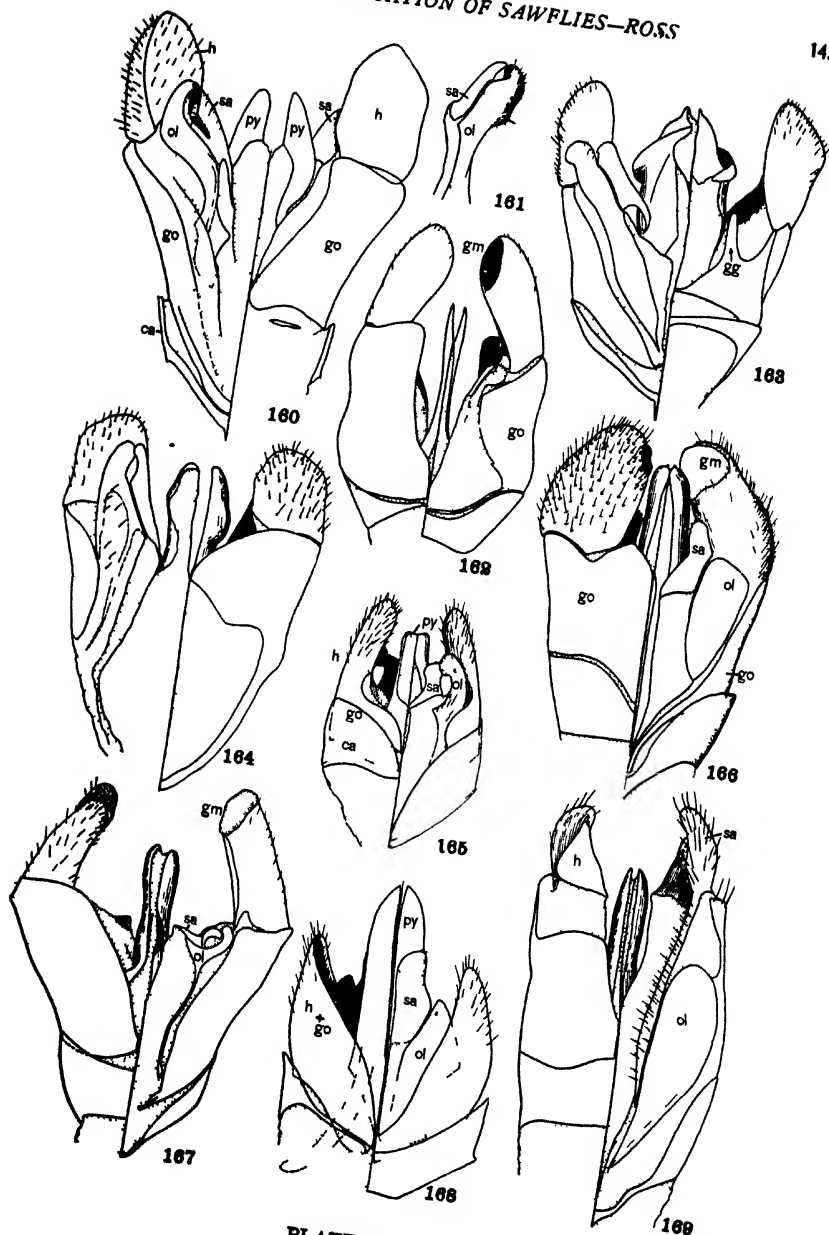


PLATE IX

PLATE X

- FIG. 170.—Hypothetical front wing of the Hymenoptera.
 FIG. 171.—Wings of *Syntexis libocedrii*.
 FIG. 172.—Front wing of *Pleroneura* sp.
 FIG. 173.—Anal veins in front wing of *Tremex columba*.
 FIG. 174.—Anal veins in front wing of *Caliroa cerasi* (L.).
 FIG. 175.—Wings of *Janus integer*.
 FIG. 176.—Hind wing of *Macroxyela ferruginea*.
 FIG. 177.—Wings of *Orussus* sp.
 FIG. 178.—Hind wing of *Arge* sp.
 FIG. 179.—Front wing of *Tremex columba*.
 FIG. 180.—Hind wing of *Taxonus epicera* (Say), showing peripheral vein.

Abbreviations

<i>a</i>	anal cross-vein	<i>m</i>	median axillary sclerite
<i>1A</i>	first to fourth anal veins	<i>M</i>	media and its branches
<i>2A</i>		<i>M₁</i>	
<i>3A</i>		<i>M₂</i>	
<i>4A</i>		<i>m-cu</i>	
<i>C</i>	costa	<i>1m-cu</i>	medio-cubital cross-veins
<i>Cu</i>	cubitus and its branches	<i>2m-cu</i>	
<i>Cu₁</i>		<i>R</i>	radius and its branches
<i>Cu₂</i>		<i>R₁</i>	
<i>Cu_{1a}</i>		<i>R₂</i>	
<i>Cu_{1b}</i>	branches of cubitus 1	<i>R_s</i>	radial sector
<i>cu-a</i>	cubito-anal cross-vein	<i>r-m</i>	radio-medial cross-vein
<i>cv</i>	cross-vein	<i>Sc</i>	subcosta and its branches
<i>h</i>	humeral cross-vein	<i>Sc₁</i>	
<i>ham</i>	hamuli	<i>Sc₂</i>	

PLATE XI
FRONT WINGS

- FIG. 181.—*Hemitaxonus dubitatus*.
FIG. 182.—*Dolerus unicolor* (Beauv.).
FIG. 183.—*Selandria vanduzeei* (Roh.).
FIG. 184.—*Adelesta nova* (Norton).
FIG. 185.—*Caliroa cerasi*.
FIG. 186.—*Allantus cinctus*.
FIG. 187.—*Phyllotoma nemorata* (Fall.).
FIG. 188.—*Tomostethus multicinctus* Rohwer.
FIG. 189.—*Fenusa pumilla* (Lep.).
FIG. 190.—*Tethida cordigera*.
FIG. 191.—*Hoplocampa* sp.
FIG. 192.—*Lycaota sodalis*.
FIG. 193.—*Nematus ventralis* Say.
FIG. 194.—*Zaschizonyx montana*.
FIG. 195.—*Kerita fidala* Ross.
FIG. 196.—*Tenthredo rufopectus* Norton.

Abbreviations same as for Plate X

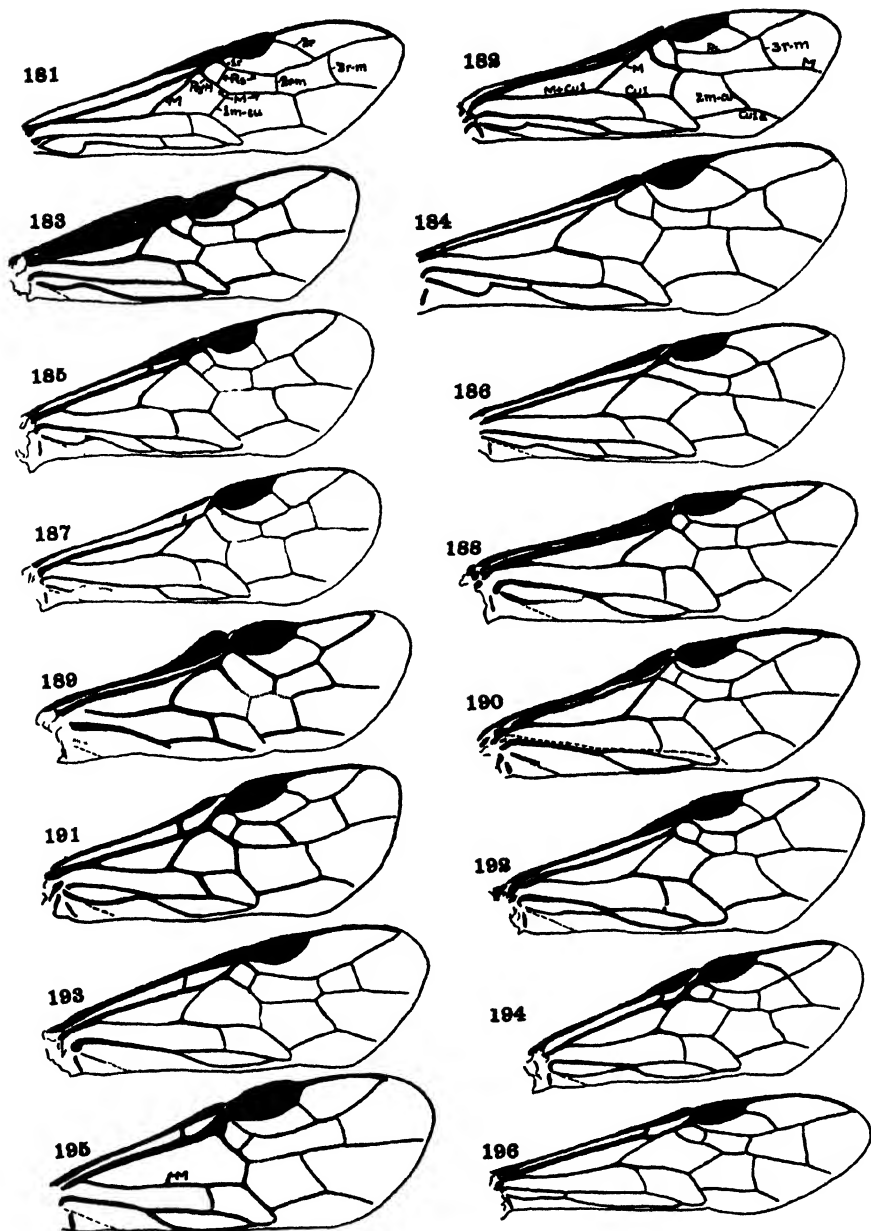


PLATE XI

PLATE XII

- FIG. 197.—Anal veins of front wing of *Tenthredo mellicoxa*.
 FIG. 198.—Anal veins of front wing of *Nematus ribesii* (Scop.).
 FIG. 199.—Anal veins of front wing of *Macrophya formosa*.
 FIG. 200.—Anal veins of front wing of *Hemichroa crocea*.
 FIG. 201.—Anal veins of front wing of *Zaschizonyx montana*.
 FIG. 202.—Anal veins of front wing of *Hoplocampa* sp.
 FIG. 203.—Anal veins of front wing of *Caliroa aethiops* (Fabr.).
 FIG. 204.—Anal veins of front wing of *Adelesta nova*.
 FIG. 205.—Anal veins of front wing of *Phyllotoma nemorata*.
 FIG. 206.—Anal veins of front wing of *Tomostethus multicinctus*.
 FIG. 207.—Anal veins of front wing of *Metallus rubi* Forbes.
 FIG. 208.—Anal veins of front wing of *Tethida cordigera*.
 FIG. 209.—Anal veins of front wing of *Fenusa pusilla*.
 FIG. 210.—Anal veins of front wing of *Blennocampa rubi* (Harris).
 FIG. 211.—Front wing of *Caliroa aethiops* showing the nomenclature of the cells.
 FIG. 212.—Head of *Lyrola brunniventris* (Cress.), dorsal view.
 FIG. 213.—Head of *Sterictiphora apios* Ross, dorsal view.
 FIG. 214.—Portion of front wing of *Sterictiphora apios*.
 FIG. 215.—Tarsal claw of *Atomacera debilis* Say.
 FIG. 216.—Tarsal claw of *Lyrola brunniventris*.
 FIG. 217.—Tarsal claw of *Sterictiphora mexicana* (Ashm.).
 FIG. 218.—Portion of front wing of *Sterictiphora niger* (Nort.).
 FIG. 219.—Scutellum of *Neodiprion lecontei* (Fitch).
 FIG. 220.—Scutellum of *Diprion polytomum* (Hartig).
 FIG. 221.—Right mandible of female *Trichiosoma triangulum*.
 FIG. 222.—Right mandible of male *Trichiosoma triangulum*.
 FIG. 223.—Anal cells of hind wing of *Sterictiphora cellularis*.
 FIG. 224.—Anal veins of the hind wing of *Sterictiphora apios*.
 FIG. 225.—Anal veins of the hind wing of *Sterictiphora zabriskiei*.
 FIG. 226.—Hind coxae of *Trichiosoma triangulum*.
 FIG. 227.—Hind coxae of *Zaraea americana*.
 FIG. 228.—Hind basitarsus and succeeding segment of *Neodiprion lecontei* (Fitch).
 FIG. 229.—Hind basitarsus and succeeding segment of *Zadiprion grandis* (Rohwer).
 FIG. 230.—Hind femur of *Trichiosoma triangulum*.
 FIG. 231.—Head of *Monoctenus fulvus* (Nort.), lateral aspect.
 FIG. 232.—Head of *Neodiprion lecontei*, lateral aspect.

Abbreviations

<i>a</i>	anal cross-vein	<i>M-Cu</i>	medio-cubital cell
<i>1A</i>	first anal vein	<i>PA</i>	proximal anal cell
<i>2A&3A</i>	second and third anal veins	<i>R</i>	radial cell
<i>Cu_{1a}</i>	cell cubitus 1a	<i>1R₁</i>	first cell radius 1
<i>Cu_{2a}</i>	cell cubitus 2a	<i>2R₁</i>	second cell radius 1
<i>DA</i>	distal anal cell	<i>3R₁</i>	third cell radius 1
<i>1M</i>	first medial cell	<i>1R₂</i>	first cell "R ₂ "
<i>2M</i>	second medial cell	<i>2R₂</i>	second cell "R ₂ "
<i>3M</i>	third medial cell	<i>3R₂</i>	third cell "R ₂ "

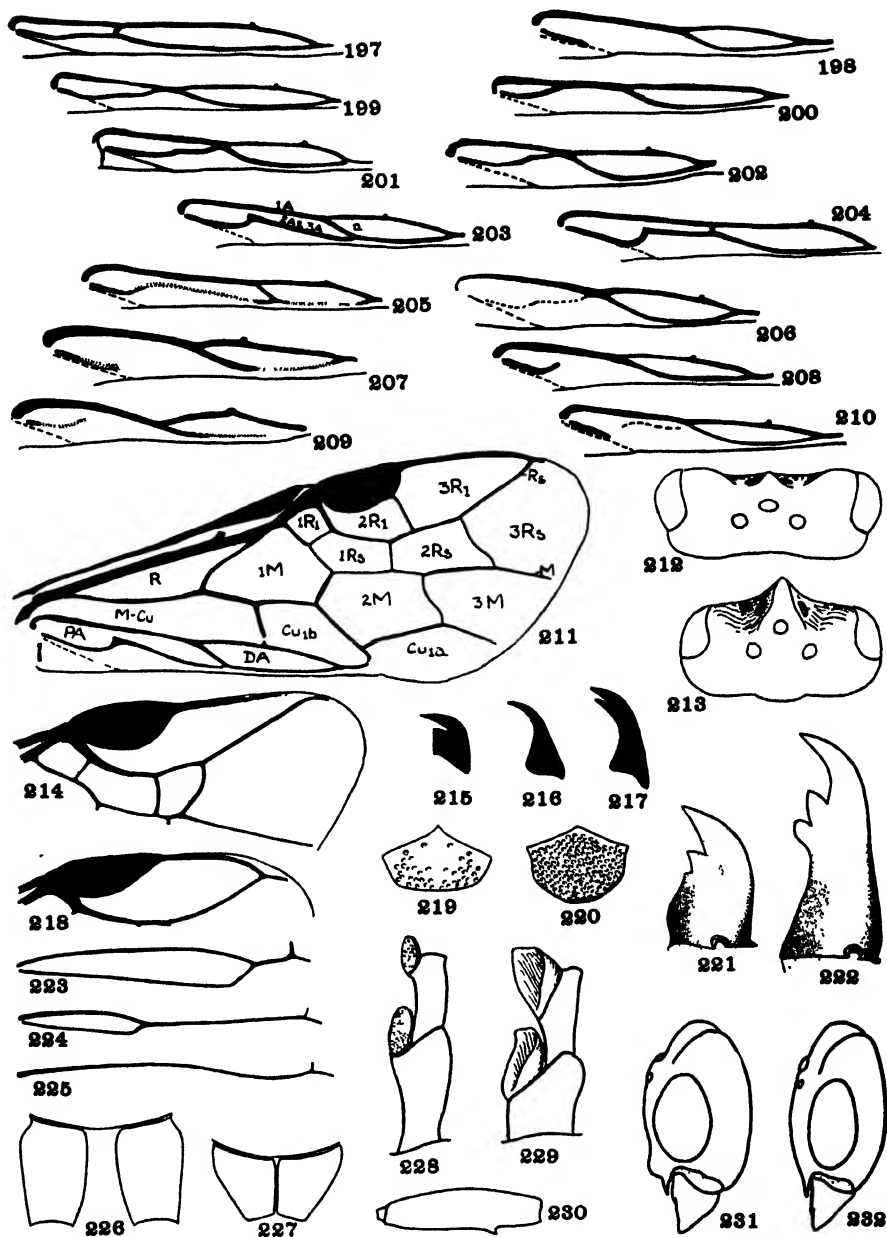


PLATE XII

PLATE XIII

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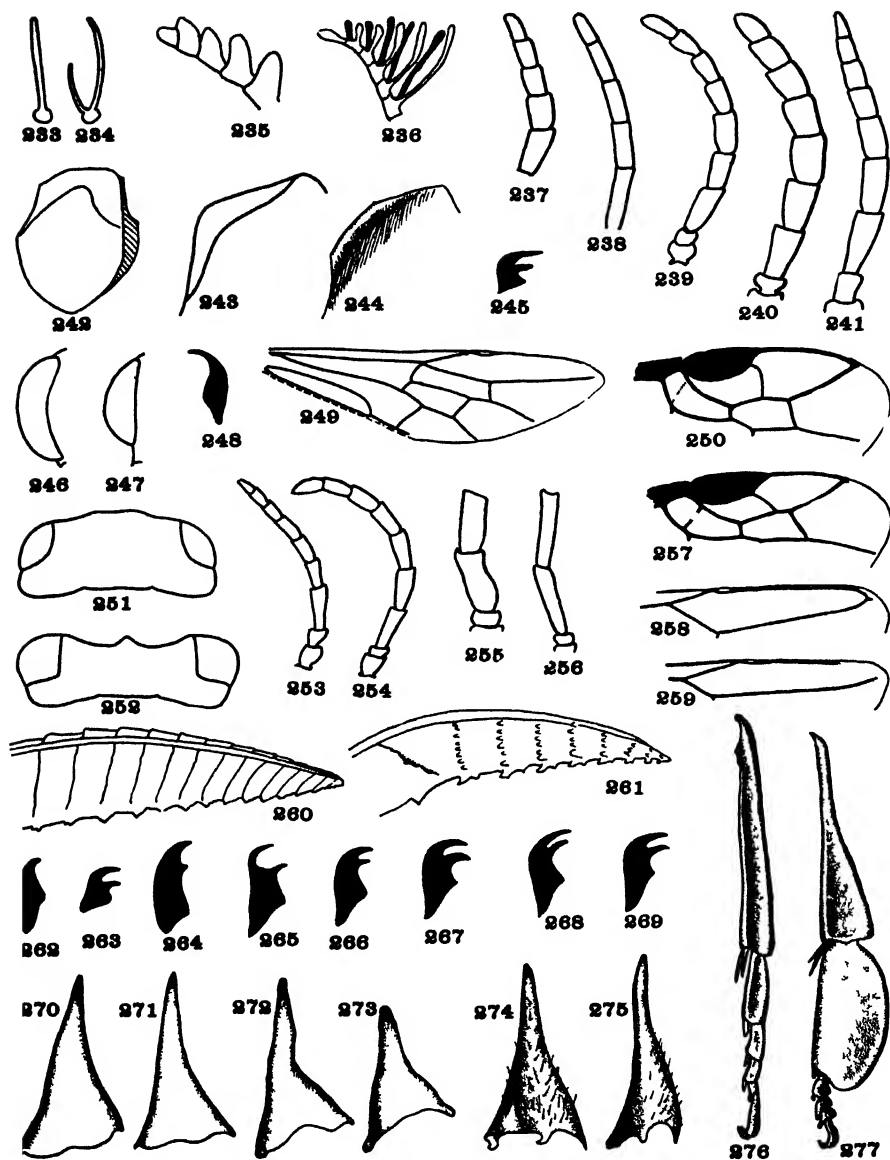


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- FIG. 278.—Antenna of *Adelomos cleone*.
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Abbreviations

- 1A first anal vein
 2A&3A second and third anal veins
 r, 2r radial and second radial cross-veins, respectively

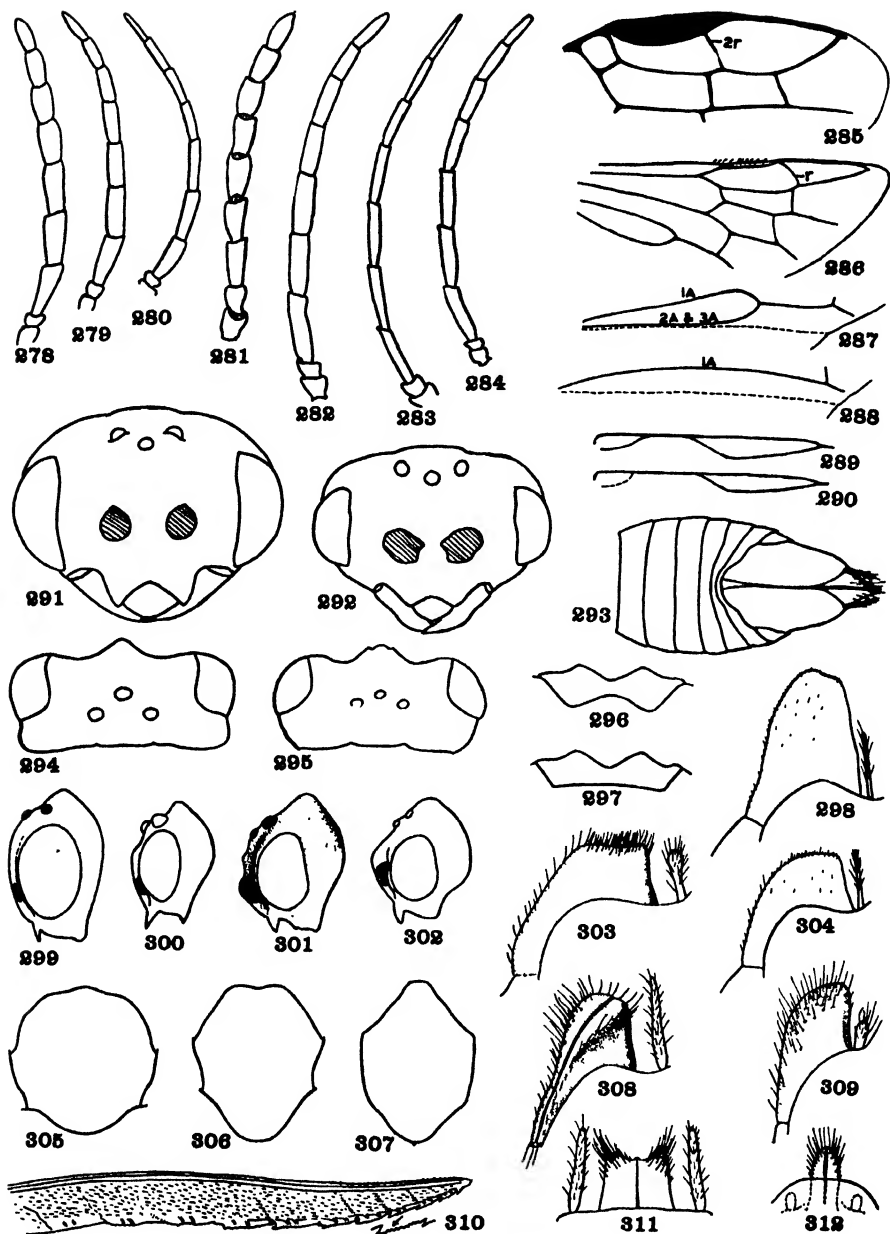


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- FIG. 313.—Penis valve of *Pristiphora chlorea*.
FIG. 314.—Penis valve of *Pristiphora erichsoni*.
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FIG. 321.—Clypeus of *Empria multicolor* (Nort.).
FIG. 322.—Clypeus of *Ametastegia tener* (Fall.).
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FIG. 348.—Hind tarsi of *Allantus cinctus*.

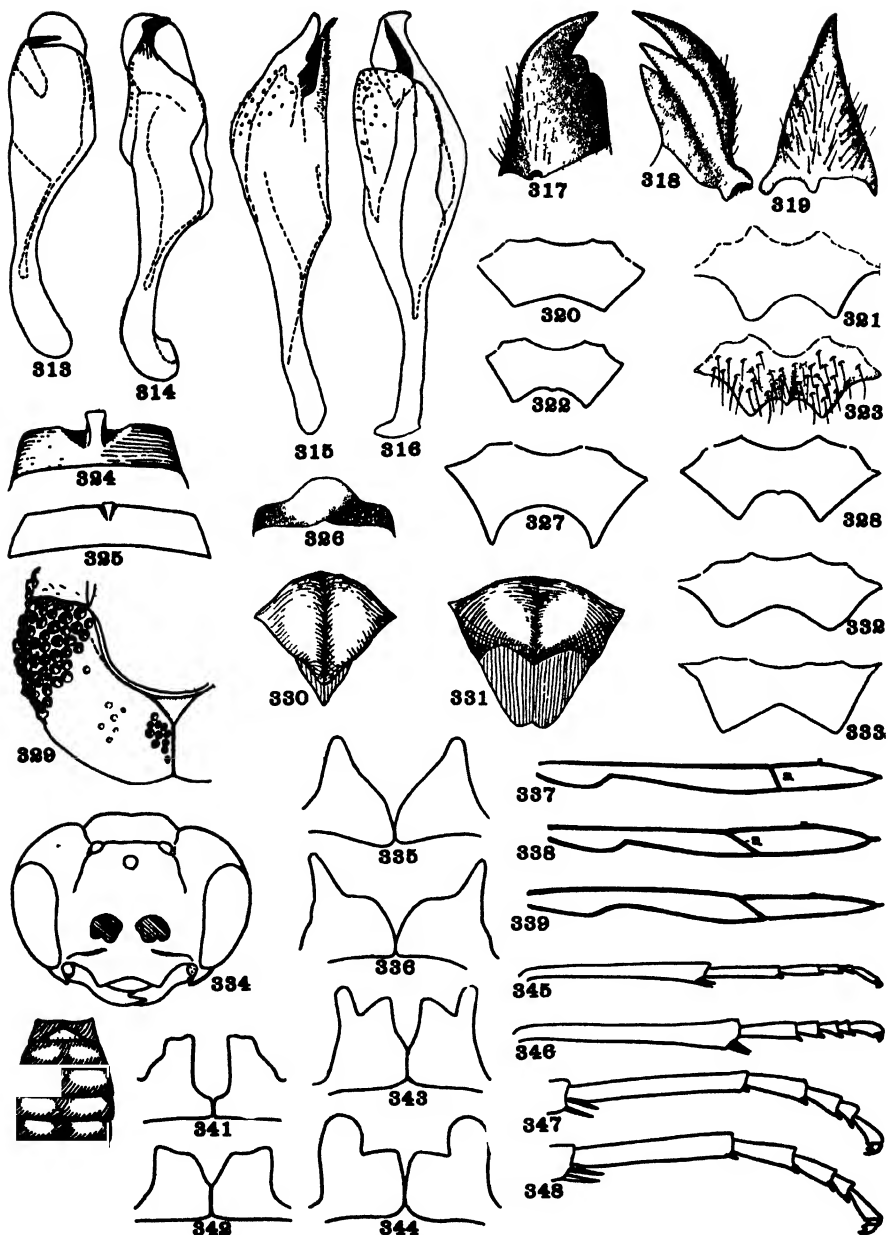


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- FIG. 349.—Antenna of *Tethida cordigera*.
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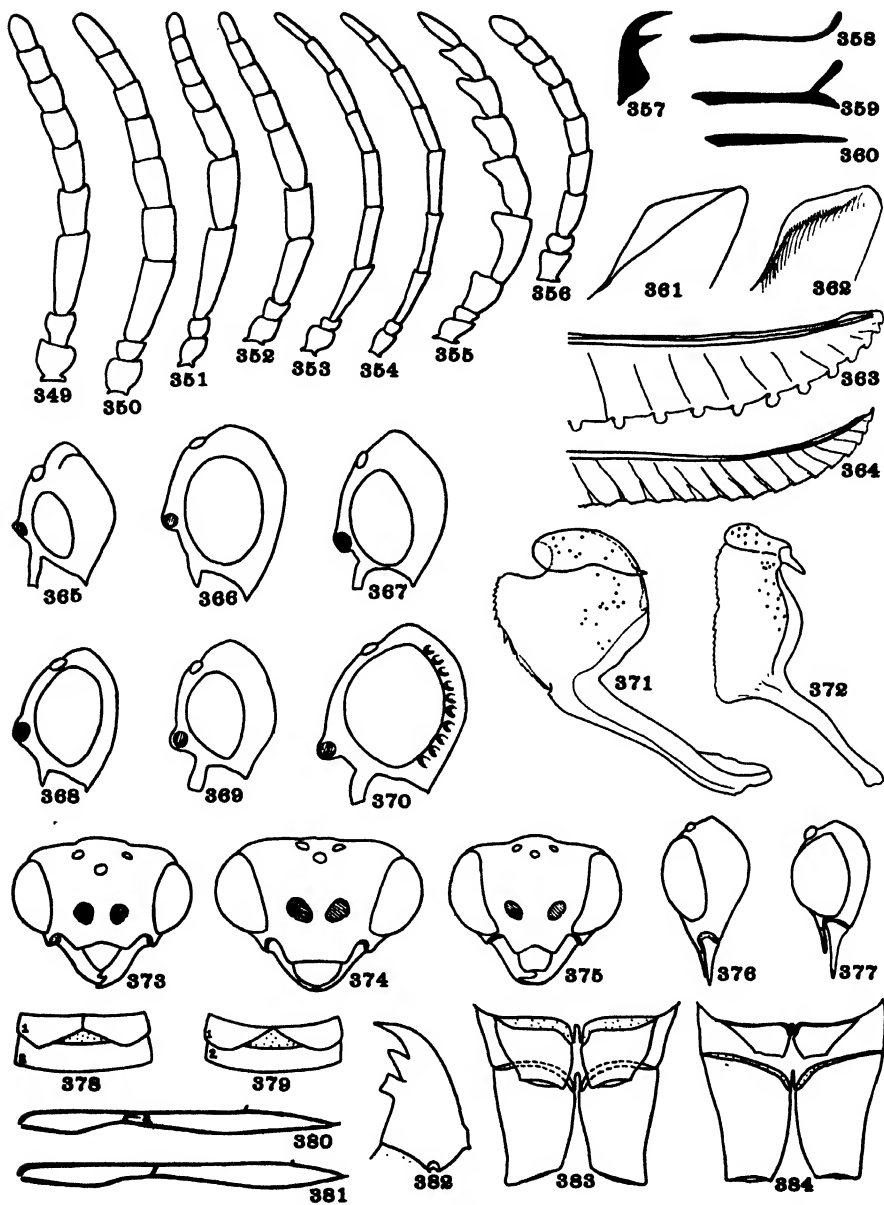


PLATE XVI

PLATE XVII

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Abbreviations

M media
*Sc*₁ subcosta 1
*Sc*₂ subcosta 2
*R*_s radial-sector

*R*₁ first branch of radial sector
*R*₂ second branch of radial sector
2r second radial cross-vein

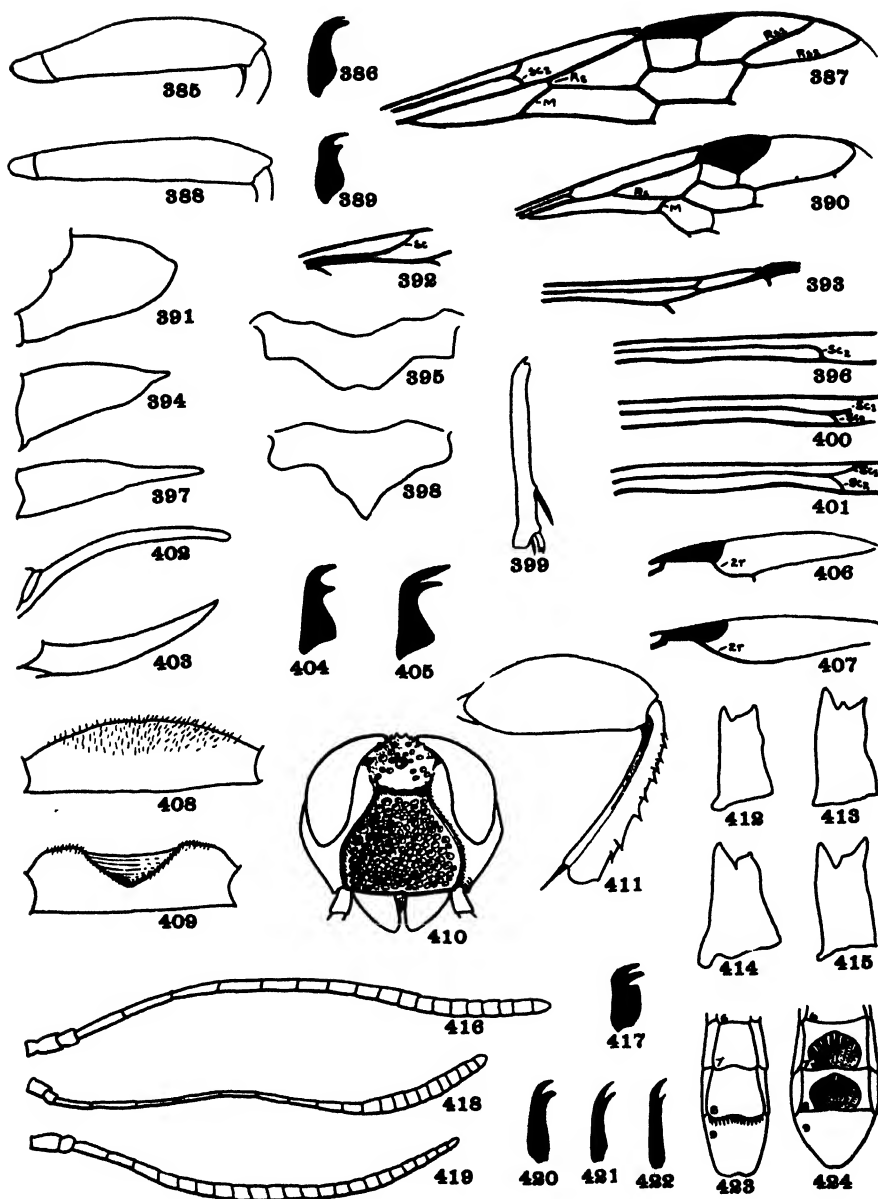


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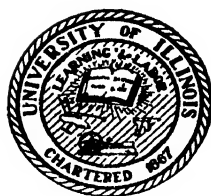
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STUDIES ON THE BIOLOGY OF THE CRAYFISH
CAMBARUS PROPINQUUS GIRARD

WITH 46 GRAPHS

BY
WILLIAM CARL VAN DEVENTER

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
UNIVERSITY OF ILLINOIS

No. 509

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Mrs. Hugh R. Smith, of Akron, Ohio, kindly consented to allow the writer to refer to her unpublished research material on *Cambarus propinquus*, most of which was compiled during 1910 and 1911 in the same general area in which the writer's research was conducted.

The main portion of the bibliographic work in connection with this study was carried on in the library of the University of Rochester while the writer was serving as field biologist for the Monroe County Park Commission, at Rochester, New York. The cooperation of the officials of the library, and of Mr. F. T. Burke, Executive Secretary of the Commission, made possible the completion of the work.

INTRODUCTION

In spite of the fact that the crayfishes are widely used for laboratory studies, very little work has been done on the developmental cycles of individual species in particular areas. Studies of seasonal changes have been almost wholly neglected. The available information concerning maximum size and length of life is of the most fragmentary sort and has in most cases been based upon observations of animals in aquaria and under unnatural conditions.

This lack of specific and detailed information is not peculiar to the crayfishes. Van Cleave (1932) has pointed out that the life cycles of very few species of animals have been carefully studied. Some forms possessing economic importance and forms causing disease have received attention, but others which are equally conspicuous have been relatively neglected so far as life history studies are concerned.

In many cases a more or less heterogeneous collection of material has been lumped together as knowledge of the life cycle of "the earthworm" or "the crayfish" and has been accepted as such in the absence of more complete studies. As was further shown by Van Cleave (1932) the general acceptance of such studies may be traced in part to an assumption that species which are closely related taxonomically have identical life histories. Such an assumption is unwarranted since careful investigation of any group of related species shows that the life histories of individual species of the group may differ markedly from one another in details. The most that can be expected in studying related species is the occurrence of parallelism in the main points of their life cycles.

The group of the American crayfishes first attracted the attention of zoologists near the middle of the nineteenth century. Girard, in 1852, published a short article in the Proceedings of the Philadelphia Academy of Natural Sciences under the title of "A Revision of North American Astaci with Observations on Their Habits and Geographical Distribution." In this article he named a number of new species, of which he gave brief and very inadequate descriptions. Hagen (1870) published a "Monograph of American Astacidae," which was very comprehensive, and which makes mention for the first time of the sexual "forms" of the male in the genus *Cambarus*. This phenomenon was further elaborated upon by Faxon (1884) who first gave the true explanation of its occurrence. Faxon (1885) published a "Revision of the Astacidae," bringing together existing information regarding species and localities. This work also contains observations on the young of three species of crayfish *C. clarkii*, *C. gracilis*, and *C. bartonii*. Andrews (1895) described in detail the process of conjugation and egg laying in *C. affinis*. In 1902, Steele published detailed observations on the young of *C. virilis*. Ortmann (1905)

revised the classification of the genus *Cambarus* by creating within it six subgenera, and in 1906 he published a very good life history of *C. obscurus*. Andrews (1907) published a comprehensive description of the appearance and growth of the young of *C. affinis*. This contribution was based, however, entirely on observations made in the laboratory.

Andrews' work embodies the chief observations on crayfish life history which have been incorporated in the textbooks of zoology in this country. All too often the student is led to think that the observations of Andrews on a single species are valid in detail for all species of the genus *Cambarus*.

In the present study a detailed and extended investigation has been made of the life cycle of a particular species of crayfish in a closely circumscribed locality. The particular species selected for the present study was *Cambarus propinquus* Girard. This is the most common of the crayfishes on the eastern side of the Ohio-Mississippi watershed in Illinois. It is found abundantly in small streams of the area, and is available for observation and collection at all seasons of the year.

METHODS

The methods used throughout the course of this work were observational and statistical. The intention was to lay emphasis on the study of the animals in their natural habitat and under natural conditions, with the hope of thus obtaining more accurate and significant data than those obtainable by studying the animals under laboratory conditions.

When the animal is removed from its natural environment and taken into the laboratory, the conditions under which it is placed are at best but a poor imitation of those which it normally encounters. Such innumerable, intricate environmental relations exist in nature that it would be hardly possible for an experimenter to duplicate them in a laboratory, even if the workings and interrelations of all environmental factors were understood. The reactions of an animal throughout the course of its life history come about as a result of the totality of all environmental relations plus the internal factors inherent in the animal itself. Therefore, any laboratory study of a life history problem, at least of the life history of a relatively large, free-moving species, is, in the writer's opinion, open to question. For this reason, in the carrying out of this work, it seemed best to rely on intensive field study.

According to the original plan of investigation, it was intended that collecting and observational trips should be made to the area under study at intervals of exactly two weeks. Circumstances, however, interfered with the fulfillment of this schedule. Periods of high water sometimes made collecting impossible, and numerous other factors precluded ad-

herence to an absolute schedule. However, at some particularly significant periods, as during the egg-carrying season in the spring, it was sometimes possible to make weekly collections and observations.

When collections were taken, field notes were made regarding environmental conditions and the relations of the crayfishes to their habitat. Particular attention was paid to their position with regard to the stationary features of the environment, and the degree and kind of activity in which they were engaged.

Collections were made by either of two methods. During the summer and early fall the animals could be taken with a dip net. This method was especially useful during early summer when the season's young were small, although adult individuals were obtained at the same time. During the late fall, winter, and early spring it was found more satisfactory in most cases to use a minnow seine. By the use of the seine a larger area of stream bottom could be covered, and the sampling over the area could be done more thoroughly. A variation of the first-mentioned method was the "still-hunt." This was used occasionally on sunny days in the winter when the water was exceptionally clear. At such times the crayfishes could easily be seen sitting on the bottom, or partially concealed under stones, and could be picked up one at a time, either with a dip net or by hand.

From the beginning of the present study the desirability of obtaining information regarding particular individuals was realized, but limiting factors seemed to preclude this under conditions of nature. The important part played by ecdysis in the physiology of the animals and particularly in the growth processes eliminated the possibility of attaching tags of any sort to the body, and likewise ruled out the possibility of applying any mark for later recognition on the shell by means of paint or pigment. Furthermore, the powers of regeneration are so marked in crayfishes and accidental injury is of such frequent occurrence that removal of appendages or parts of appendages is of no value for later recognition of individuals. This method was attempted during the second year of the study, but without success. Therefore, all of the previously utilized methods of marking individuals for recapture and study were impracticable for use in this study of crayfishes.

In consequence of this the collections which were taken were treated statistically. The living animals of each collection were separated according to sex. The males were further studied and notes were taken for each individual as to the "form" of the copulatory appendages. Seasonal limitations of occurrence of the "first form," "second form," and juvenile males were thus established for the habitat under consideration.

It seemed desirable to obtain a single measurement on each individual which would serve as an index to its size and general development, and

also one which could be used equally well for both sexes. The works of Huxley (1924), Shaw (1928), Bush (1930), Bush and Huxley (1930), and others in connection with heterogonic growth of different body parts in the group of Crustacea show that the growth rates of different body parts bear relations to one another which are definite and mathematically expressible. Thus the relation of the rate of growth of the chela of the male to the rate of growth of the body as a whole can be expressed as a constant, the chela increasing in absolute size more rapidly than the body, though at a constant rate. Such relations, however, are chiefly discernible in connection with secondary sexual characters, and differ radically in the two sexes. With grosser body measurements in which the two sexes do not differ the relations are relatively constant throughout life, and may be used as indices of individual and group development.

Therefore, it was necessary to choose a body measurement of relatively gross nature, and one in which the sexes showed no apparent difference in regard to relative size or form. In addition it was necessary to choose a measurement which could be taken in the field with a minimum of time and effort, and one which would not be affected by the movements of the animal during the process of measurement. The length of the cephalothorax from the tip of the rostrum to the anterior end of the abdomen was chosen as the measurement which best fitted all requirements. Furthermore, this measurement could be easily translated into terms of approximate body length, since it represents 49% of the total body length in all periods of the life history after the young become free-swimming. For purposes of general comparison with published data in which the only measurement given was the total body length, the writer has found it practicable to consider the cephalothorax length as one-half of the total body length.

The length of the cephalothorax was used by Smith (1910-11) in her unpublished studies of *C. propinquus* at Urbana, Illinois, and more recently by Creaser (1933 and 1934) in his studies of the same species in Michigan.

In the present study the measurements were taken in the field, and as soon as the necessary observations were completed the animals were returned to the water. The individuals were measured by means of vernier calipers, and the measurements were recorded to the nearest tenth of a millimeter. In conformity with the general intention to preserve as nearly natural conditions as possible, the animals were handled only twice during the entire operation and were held out of the stream for as short a period as possible.

The measurements of the population sample examined on each collecting trip were plotted graphically, using one millimeter as the unit of construction. In reducing the fractional measurements to one milli-

meter size classes, those from 9.6 to 10.5 were counted as 10, those from 10.6 to 11.5 as 11, etc. In constructing the graphs it was found most satisfactory to let the abscissas represent cephalothorax lengths, and the ordinates represent numbers of individuals. This seemed to result in the separation of the population into natural size groups. The modes of these size groups were then plotted on a composite graph (see Graph 3) in which the ordinate was made to represent the position of the modes in millimeters, while the abscissa was made to represent time in weeks. By connecting the points denoting the same size groups in different collections, these size groups came to be represented by lines. They could then be followed in their growth and development through the season and could be related to molting and other life history phenomena.

In the study of each population sample, separate plottings were made for the cephalothoracic measurements of the members of the two sexes. These plottings were made by the same method which was used for plotting the measurements of the general population, and the distribution curves for the males and females in each collection were placed on the same sheet as the distribution curve for the general population taken in the collection. This placed the curves in a position convenient for purposes of comparison.

A detailed account of the development of statistical methods of life history study is given by Van Cleave (1931). The particular method used in the present study is an adaption of the method used by Van Cleave and Markus (1929) in the study of the blunt-nosed minnow, *Hyborhynchus notatus*; by Foster (1932) in the study of the fingernail shell, *Sphaerium solidulum*; and by Van Cleave and Lederer (1932) in their study of the snail, *Viviparus contectoides*. Similar methods were used by Creaser (1933 and 1934) in his study of *C. propinquus* in Michigan.

DISTRIBUTION OF THE SPECIES

The specimens of *C. propinquus* which Girard first described came from Lake Ontario and western New York. The species is now known to occur also in Pennsylvania, Ontario, Quebec, Ohio, West Virginia, Indiana, Michigan, Illinois, Wisconsin, Iowa, Minnesota, and Nebraska. It is found chiefly and most abundantly in the Great Lakes drainage (Ortmann, 1905 and 1906; Graenicher, 1913; and Turner, 1926). However, it has migrated extensively into the Ohio and Mississippi River systems (Ortmann, 1905 and 1906) and even into the Missouri River system (Engle, 1926).

It is found in the Great Lakes drainage of New York and southern Canada (Ortmann, 1905); in the Great Lakes drainage of Pennsylvania and Ohio (Ortmann, 1906); and also in a restricted area of southern

Ohio (Turner, 1926). It occurs in the extreme northern tip of West Virginia (Newcombe, 1929). It is found throughout the states of Indiana and Michigan (Hay, 1896; Pearse, 1910). It is most abundant in the Great Lakes drainage of Wisconsin, but also occurs to some extent in the Mississippi drainage of that state (Graenicher, 1913). It occurs in the Mississippi drainage of Iowa and Minnesota (Ortmann, 1905), and colonies of it occur in the Big Blue River drainage of southeastern Nebraska, which is a part of the Missouri River system (Engle, 1926).

In Illinois the species is found in both the Mississippi and Ohio River drainage systems, and occurs in both the northern and southern sections of the state. Harris (1903) lists it as occurring in the Illinois River drainage in McLean, Tazewell, and Macon counties. The writer has in his possession a collection of *C. propinquus* taken by Mr. John Cralley in the fall of 1932 in the vicinity of Carmi, which lies within the Ohio River drainage of southern Illinois, showing that the species occurs in that section of the state also.

C. propinquus gives place in Ohio (to the south of the Great Lakes drainage) to *C. propinquus sanbornii*, and this in turn gives way in central and southern Pennsylvania to *C. obscurus*. These three forms constitute a very closely interrelated group. It is the belief of Ortmann (1905 and 1906) that these three types of crayfishes originated in the three principal tributaries of the Eriean River, a pre-glacial river which drained most of the present-day Ohio Valley and Great Lakes basin and emptied into the Gulf of St. Lawrence. With the temporary damming of the old river outlet during the glacial period and the formation of a new drainage outlet to the southwest (the present Ohio), the three types of crayfishes came to occupy the lower, middle, and upper portions of the Ohio River valley.

C. propinquus, being more strategically located in relation to the newly exposed territory from which the ice had receded, recolonized the Great Lakes basin, and migrated westward into the Mississippi and Missouri River drainage systems, while *C. propinquus sanbornii* and *C. obscurus* did not increase their range to any marked extent.

HABITAT

The principal collecting area consisted of a section of about 150 yards of a small stream in the north edge of Urbana, Illinois. This stream is known locally as the Saline Drainage Ditch. It rises in the northern part of Champaign County, Illinois, and flows into the Vermilion River. This in turn empties into the Wabash River and forms a part of the Ohio River system. Studies were carried on at this collecting station during two years, from June, 1932. to June, 1934.

At the place where the collections were taken the stream contains two small areas of rapids, but otherwise it is very slow flowing. In the rapids the bottom consists of numerous stones lying upon a substratum of coarse gravel. In other parts of the stream the bottom consists of a mixture of silt and sand, over which are scattered stones of various sizes. When the stream is at a normal level the depth in the collecting area varies from a few inches at some points along the edge to about three feet in the deepest places.

The shallow areas near the banks support a rank growth of semi-aquatic vegetation during the summer. Other vegetation consisting of weeds, sedges, and grasses grows on the banks at the edge of the water and overhangs into the water. The banks are either unshaded or only partially shaded by trees and shrubbery.

In the late fall the stream becomes nearly filled in places with drifts of water-soaked dead leaves. This is particularly true if there is a low water level during October and November. Such leaf drifts persist during most of the winter behind clusters of dead vegetation and in the bottoms of the deeper pools.

The stream was not ice bound for any considerable time during either of the winters while the study was being conducted (1932-33 and 1933-34). During each winter there were a few times when it was necessary to break the ice in order to secure collections, but even at such times the areas of rapids were open.

The stream is subject to considerable variation in amount of flow on account of the fact that it is dependent on surface run-off rather than on springs or other relatively constant sources of supply. During the spring seasons of 1933 and 1934 there were periods of high water during which the collection of crayfish in large quantities was difficult or impossible. Similarly, periods of prolonged dry weather caused a marked fall in the water level.

During the fall of 1932 supplementary studies were carried on at a collecting station on Stony Creek, a small stream in the western part of Vermilion County, Illinois, about 25 miles east of Urbana, Illinois. This stream also flows into the Salt Fork of the Vermilion River.

This stream is rock-bottomed, and in general is much more swift flowing than the Saline Drainage Ditch. It consists of extensive areas of rapids with deep pools between. However, it, likewise, is subject to wide fluctuations in amount of flow, depending on local rainfall.

The portion of the stream from which the collections were taken consists of two habitats, an area of rapids and a pool located at the foot of the rapids. The rapids measure from 6 to 12 inches in depth and the pool from 2 to 3 feet in depth when the stream is at a normal level. The

vegetation at the edge of the stream is relatively rank, and is of the same general character as that described for the Saline Drainage Ditch. Here, however, the banks are low, and in themselves offer little or no protection to aquatic organisms. The water is very clear, and carries very little sediment even in flood times.

RELATION TO ENVIRONMENT

The species of *Cambarus* may be classified into two major groups on the basis of their habitat preferences. These two groups are: (1) those species which spend a part or all of their time on lowlands in burrows which extend down to ground water; and (2) those species which are always found in open water, either small streams, rivers, or lakes. *C. propinquus* belongs to the second of these two classes.

Individuals of this species do not make burrows, even during periods of adversity, although occasionally they may make tunnel-like excavations in the banks of streams, slightly below water level (Hay, 1896; Harris, 1903; Engle, 1926). Therefore, except for the possibility of occasional overland migrations, they are confined to permanent bodies of water, and accomplish their entire life cycle within the stream, lake, or pond in which they are found. Within a particular body of water, however, they exhibit very definite relations to local variations of habitat, and these relations vary markedly at different seasons of the year, and at different periods of the life cycle.

During the summer months the young crayfish are found in the surface layer of water among the weedy vegetation which grows along the edge of the stream. They usually select the shallower areas where the vegetation is more abundant, but they are also found in the surface water over deeper areas, provided vegetation is present.

The adults select the bottom of the stream at all seasons, and are rarely taken near the surface. In the summer they are usually found under stones or other objects in the shallower places, either along the banks or in the shallower pools and rapids. Since the young crayfish are also found along the banks during the summer months, collections taken in summer along the shallow, weedy portions of the stream yield representative samples of all sizes and age groups. However, such collections are really taken from two distinct strata of crayfish population: (1) the bottom-dwelling adult population; and (2) the surface-dwelling juvenile population.

In late summer the young crayfish leave the surface layer of water and select the shallow areas of stream-bottom as do the older individuals. Therefore, there is no appreciable difference in habitat relations between the adults and the season's young during August and early September.

After the middle of September all of the crayfish show a definite tendency to leave the shallow areas and resort to the deeper pools. This tendency is most marked, however, among the large and mature individuals. Not only the class which has been adult during the summer but also those among the season's young which have just attained maturity show a more marked tendency to leave the shallow water than do the immature individuals. Thus a partial segregation of mature and immature individuals takes place.

TABLE 1.—DISTRIBUTION OF MATURE AND IMMATURE INDIVIDUALS IN SHALLOW AND DEEP WATER OF STONY CREEK*

Date of collection	Mature individuals			Immature individuals		
	Number collected	Percent-age in deep water	Percent-age in shallow water	Number collected	Percent-age in deep water	Percent-age in shallow water
Oct. 2, 1932.....	39	51.7	48.3	100	25.	75.
Oct. 13, 1932.....	30	80.	20.	100	41.	59.
Oct. 27, 1932.....	50	60.	40.	70	42.8	57.2
Nov. 10, 1932.....	33	60.7	39.3	84	44.	56.

*All collecting on Stony Creek had to be done with a dip net, since the bottom is too stony for a seine to be used successfully; and the dip net had to be used "blindly" in the deep water, while in the shallow water the individuals could be seen and dipped out to better advantage. Since there was a preponderance of mature individuals in the deep water, and a preponderance of immature individuals in the shallow water, this unequal sampling resulted in a preponderance of immature individuals in all collections taken during the fall.

Table 1 shows the distribution of mature and immature *C. propinquus* taken at Stony Creek during October and November, 1932 as related to shallow and deep water habitats. The size of 20 mm. cephalothorax length was taken as the approximate lower boundary of sexual maturity in both sexes.

It will be seen that in these collections the segregation was only a partial one, representing a difference in relative abundance of the two size classes in the two habitats, rather than a clear-cut segregation. However, in every collection the major portion of the mature population was taken in the deeper water, while the major portion of the immature population was taken in the shallower water.

This tendency towards segregation was also found among the crayfish population of the Saline Drainage Ditch. In a collection of 75 individuals taken from this stream on November 17, 1932, 63.3% of the mature group were found in the deep water, and 36.7% were found in the shallow; while of the immature group only 31.8% were found in the deep water, and 68.2% in the shallow.

With the beginning of winter this tendency towards segregation largely disappears. Most individuals of all size groups leave the shallow areas and conceal themselves in dead leaf drifts or under stones in the

deeper portions of the stream. Smith (1910-11) found as many as six individuals partially buried in the mud and detritus under one small stone in November. She found further that there was a tendency for them to seek the shelter of larger stones and to bury themselves more deeply in the mud, as the winter became more advanced.

The crayfish of this species show some activity all during the winter. However, in the winter the effects of environmental factors which regulate the time and amount of activity become more noticeable. Apparently one of the principal factors regulating the winter activity of *C. propinquus* is sunshine. There is some correlation between sunshine and amount of activity of this species at all seasons. Collections taken on sunshiny days, even during the summer, invariably yielded better results than did those taken on days when the sun was not shining. During the late fall and winter, however, the activity of the animals becomes even more closely correlated with sunshine.

After the middle of November, if the sun is shining, the crayfish show a limited amount of activity during the middle of the day, but none at all at any other time. This period of activity begins at about 11:00 A.M., and lasts until about 2:00 P.M. On cloudy days, or at times other than near mid-day when the sun is shining, the animals remain concealed.

During the late fall and winter, therefore, the only time when collections could be secured satisfactorily was near mid-day on sunshiny days. The temperature in such cases apparently had little or no effect on the result of the collections. Table 2 shows the results of five typical late fall and winter collections in which the number of crayfish obtained is correlated with the time required to make the collection, the temperature of the water, and the presence or absence of sunshine. All of the collections included in the table were taken near the middle of the day.

In winter the size of collections furnishes a very good indication of the amount of activity of the crayfish population at the time the collections are made, since only those individuals which are active in the water, or are sitting unprotected on the stream bottom, or are concealed

TABLE 2.—RELATION OF SIZE OF COLLECTIONS IN WINTER TO TEMPERATURE AND SUNLIGHT

Date of collection	Number of individuals secured	Time required (hrs.)	Temperature of water (C.)	Character of day
Nov. 18, 1933.....	64	1½	4°	Sunshiny
Dec. 6, 1933.....	68	1½	6°	Sunshiny
Dec. 20, 1933.....	30	1¾	5°	Cloudy
Jan. 6, 1934.....	31	2	4°	Cloudy
Jan. 20, 1934.....	70	2	5°	Sunshiny

under small stones are likely to be taken with the seine. The crayfish which are buried in the mud or are concealed under large stones are not likely to be collected. Therefore, the close correlation of the size of collections with the presence or absence of sunshine which is shown in the above table indicates an equally close correlation of diurnal activity with sunshine.

The fact that *C. propinquus* is to some extent diurnally active, and the apparent close relation of its diurnal activity to sunshine is at variance with some of the literature on the activity of crayfishes. Chidester (1908) found *C. bartonius bartoni* negative to strong light and nocturnally active under laboratory conditions. Pearse (1910) says: "All crayfish are nocturnal in their habits. . . . They come forth at night to search for food." Newcombe (1929) says: "During the day crayfishes are usually found at rest, . . . while at night they are very active, since it is at this time that they go in search of food." However, Hay (1919) repeatedly observed *C. propinquus* feeding during the day under natural conditions, and the writer also observed individuals feeding during the day on a number of occasions, both in nature and in the laboratory.

No systematic field study was made during the present work to determine whether or not *C. propinquus* is nocturnally active under natural conditions. The individuals which were kept in laboratory aquaria, however, showed no greater tendency to be active at night than during the day. When the light was turned on at any hour of the night, they were almost always found to be sitting quietly on the sand at the bottom of the aquarium. This evidence, considered in connection with the fact that *C. propinquus* is to some extent at least diurnally active under natural conditions, and the further fact that it is undoubtedly positive to sunlight, would seem to indicate that there is no definite nocturnal rhythm of activity in this species.

THE LIFE CYCLE

TYPE OF LIFE HISTORY

Ortmann (1906) divides the species of the genus *Cambarus* into two groups on the basis of the general type of life history which they follow. He calls these two types the "cool water type" and the "warm water type." The species of the "cool water type" breed and spawn practically the whole year around, while those of the "warm water type" have a restricted breeding season. *C. propinquus* belongs to the "warm water type."

The seasonal life history of species of this type conforms to the following general outline: a fall mating season, a spring spawning season, a spring or summer period during which the males are all second form (when the copulatory appendages have temporarily lost the hard texture,

sharp points, and peculiar sculpturing which ordinarily accompany the mating season). This period is followed by a change at some time during the spring or summer by which the males again become first form as a prelude to the fall mating season. Both changes of sexual form on the part of the males occur in connection with molts.

In the following sections, detailed observations on the life cycle of *C. propinquus* will be presented, and the relation of these observations to those recorded by previous observers on this and related species will be discussed.

THE EARLIEST YOUNG

Time of Appearance.—The young appear among the free-swimming population during a very short period in May or early June. In 1933 the first young were collected on June 7th (Graph 26). In 1934, however, they were taken three weeks earlier, on May 13th (Graph 46). This time difference can be attributed to the occurrence of a generally different type of spring season in 1933 and in 1934. The spring of 1933 was cool, cloudy, and rainy, so much so that in many cases the planting of spring crops was delayed from three weeks to a month beyond the normal time. The spring of 1934, however, was relatively warm and sunshiny.

The difference in the time of the appearance of the young was due to an increase in the length of time required to hatch the eggs, rather than to a delay in the laying of them. In 1933 the first egg-bearing females were found on April 8th, and the latest on May 21st, thus making a period of 43 days during which the females were carrying eggs. In 1934 the first egg-bearing females were found on April 7th, and the latest on May 6th, making a period of only 29 days during which the eggs were carried. These periods correspond in general to the time required for the eggs to hatch, since the juvenile population, when first found, and before any factors making for differential growth have had time to take effect, forms such a homogeneous group that it is obvious that its members must all have been spawned at approximately the same time.

Andrews (1904) found a similar variation in the time required for the eggs of *C. affinis* to hatch, depending on the temperature during the time when the eggs were being carried by the female. With higher temperatures he found that the eggs hatched in five weeks after being laid, while with lower temperatures a period of eight weeks was required.

Description of Young.—At the time of their first appearance in the quantitative collections the young *C. propinquus* measure from 3.9 to 6.1 mm. cephalothorax length. This is equivalent to a total body length of approximately 8 to 12 mm. This juvenile section of the population when plotted graphically (Graph 26) forms a simple, unimodal curve with a very narrow spread. This indicates that all of the juvenile indi-

viduals are approximately the same age and represent the same general degree of development.

These young differ from the adult in having a more sharply pointed rostrum; proportionally larger and more prominent eyes; more slender chelae; and a difference in color. Also, the young crayfishes at this time have not yet developed the external sexual characters to a point where any recognition of the sex in the field is possible. The annulus ventralis of the female is not yet distinct, and the first abdominal appendages in both sexes are apparently identical, being small, short, and thread-like, resembling in general the other pleopods, though smaller and shorter. Even at this time, however, the valley of the rostrum shows the median carina which is characteristic of the species. The general shape of the body and the relative proportions of the cephalothorax and abdomen are similar to those of the adult, and the young animal swims in the same manner as the adult.

Length of the Dependent Period.—No direct observations have ever been published on the length of time during which the young of *C. propinquus* are associated with the mother after hatching. No females bearing young were taken in the collections made by the writer during the spring of 1933, and Dr. John Mizelle who carried on the work of collecting for the writer during the spring of 1934 was able to secure only a single *C. propinquus* female bearing attached young. This individual was taken on April 21, 1934, in connection with a field trip of an elementary zoology class, but it died before reaching the laboratory. The brood of this female evidently were hatched at an abnormally early date, since the majority of the adult female population were still bearing eggs on April 28th, one week later.

There are very few references in the literature to the finding of *C. propinquus* females bearing young. Pearse (1910) records finding a single female of this species with young in Whitmore Lake, Washtenaw County, Michigan, on May 29, 1898. Hay (1919) speaks of finding "one very small one with its mother" on June 7, 1901, in Lake Maxinkuckee, Indiana. Smith in her unpublished records of *C. propinquus* taken in 1910 and 1911, lists the finding of only three females of *C. propinquus* bearing young in the field, and only three others which hatched their eggs in the laboratory. She records no measurements or other observations for these.

The scarcity of records for females of this species bearing young makes it seem probable that the young remain with the mother for a relatively short time, and that during that time the female remains in seclusion and inactive. These conclusions are borne out by the evidence from the present study.

In 1933, in the collection of May 6th, all of the adult females were bearing eggs. In the following collection of May 21st only two egg-bearing females were taken, and the majority of the former egg-bearing group were absent from the active population. In the next collection, taken on June 7th, these females had reappeared in the active population along with the free-swimming young. At that time all of the adult females had completed their molt, which takes place immediately after the young are shed.

In 1934 the circumstances were similar. On April 28th practically all of the mature females were found to be carrying eggs. On May 5th only one egg-bearing female was taken and most of the former egg-carrying group were absent. In the following collection of May 13th these adult females had reappeared and were newly molted. Only a few young were taken in this collection, however, probably on account of local environmental conditions which made them less active on that day or at the time of day when the collection was taken.

The absence of a major portion of the adult females from the collection taken just prior to the appearance of the season's young in the free-swimming population indicates that these females were inactive or were in seclusion at the time the collection was made, and that they were then probably either hatching their eggs or were bearing attached young. It seems most probable that in both years this collection was taken while hatching was still in progress, and at a time when it was nearing completion, since only a few females were found in the active population which were still bearing eggs. Therefore, we may consider the date of the collection as being approximately the date of the completion of hatching for the major portion of the season's young. And since in 1933 the members of the juvenile population were all found to be of approximately the same size and degree of development at the time when they appeared in the free-swimming population, we may safely assume that the majority of the young in 1933 were hatched just prior to May 21st, and in 1934 just prior to May 5th.

Between these dates and the time of the appearance of the young in the quantitative collections there was a period of 17 days in 1933 (May 21st to June 7th) and of 8 days in 1934 (May 5th to May 13th). These periods represent the approximate lengths of time during which the young were carried by the females, together with the time required for the adult females to complete their molt after the young were shed. Some idea of the length of time required by the females to complete this molt may be obtained from the records of Smith (1910-11). In a collection taken from the stream on June 2nd she found "no females with young and a few females molted." On June 6th she found "all females

molted." This gives a period of 4 days during which a majority of the adult females were passing through the molt.

If we subtract 4 days from the 17- and 8-day periods to allow for the completion of the molt by the females which had been bearing the young, we have left periods of 13 days and 4 days respectively. These periods should represent approximately the length of time that the young were carried by the females in 1933 and in 1934. However, since the dates which we have for hatching represent the time of the completion of the hatch, it seems more justifiable to conclude simply that the period during which the young remain with the mother in this species may vary from one week or less in favorable seasons, to about two weeks in extremely unfavorable ones.

This conclusion agrees with the information obtained by Steele (1902) and by Ortmann (1906) for *C. virilis* and *C. obscurus*, both of which are closely related to *C. propinquus*. Steele (1902) found that the young of *C. virilis* remain attached to the female for 9 days or more. Ortmann (1906), in giving the life history of *C. obscurus* says: "the period during which the young stay with the mother seems to be short. . . . The young crayfishes probably do not remain with the mother much longer than a week."

Developmental Stage of Earliest Young.—In the literature on the group of the crayfishes the term "stage" is used somewhat loosely to indicate any life history period. It is more properly confined, however, to the period between any two molts. Therefore, it is equivalent to the more specific term "instar." Although the latter term is not ordinarily used in carcinological publications, it will be used in the present work because there is less likelihood of confusion in regard to its meaning, than is the case with the more general term "stage."

Somewhat varying results have been recorded in studies of different species of crayfish, pertaining to the particular instar represented by the earliest free-swimming young. Andrews (1907) found that the young of *C. affinis* remain under the abdomen of the female during the first, second, and most of the third instars, or until nearly 26 days old. At that time the larvae measured 8 mm. in total body length (corresponding to approximately 4 mm. cephalothorax length). He said of this third instar that "in general the young crayfish of this stage is now for the first time like the adult."

Andrews, therefore, believed that all *Cambarus* young are dependent during three instars. In further support of this theory he showed that the young of *C. diogenes* remain with the female until the third molt (through the third instar). In addition he quoted Faxon (1885) as having found the young of *C. clarkii*, *C. bartoni*, and *C. gracilis* still under the abdomen of the female and measuring from 7 to 10 mm. long.

Steele (1902), however, in studying the young of *C. virilis* found that the first ecdysis did not occur until 9 days after hatching. As a result of this molt the young crayfish lost most of their larval characters and assumed the general body form of the adult. They might leave the mother on occasion after this molt, but did not necessarily do so.

In describing the young *C. virilis* of this second instar, Steele said: "The rostrum is much lengthened and is no longer bent down between the eyes. The chelae have lost their recurved hooks. The abdomen and cephalothorax have assumed about the same relative proportions as in the adult. The appendages of the first abdominal somite have not yet appeared, although a minute swelling can be seen and the appendages will be set free after the next molt." In this second instar the young *C. virilis* measured 7 to 8 mm. body length (corresponding to 3.5 to 4 mm. cephalothorax length).

This description shows that the young *C. virilis* of the second instar are quite similar to the young *C. propinquus* which first appear in the quantitative collections. There are only two notable differences. One of these is the size of the young animals: 7 to 8 mm. body length for *C. virilis* as compared to 8 to 12 mm. body length for *C. propinquus*. The other difference lies in the fact that in Steele's *C. virilis* of the second instar the appendages of the first abdominal somite had not yet appeared, and did not appear until after the next (the second) molt, while in the young of *C. propinquus* when they first appear in the collections these appendages are present, though as yet they are undifferentiated. In view of these differences it seems probable that the young *C. propinquus* have already undergone two molts before they appear in the free-swimming population.

Conclusions Regarding Earliest Young.—On the basis of the foregoing observations it seems justifiable to conclude that: (1) the young *C. propinquus* remain with the mother for a relatively short time; apparently one week or less in favorable seasons, with the period extended to about two weeks in extremely unfavorable seasons; (2) that the females bearing young remain in seclusion, and are relatively inactive during the time that the young are attached; (3) that the young which first make their appearance in the quantitative collections are probably in the third instar, having left the mother at, or shortly after, the occasion of the second molt; and (4) that, in favorable years at least, these first two molts have occurred in rapid succession.

SEX RECOGNITION

In the season of 1933 it was possible to recognize the sex of the juvenile population in the field for the first time in the collection of July

10th. This was more than a month after the season's young first appeared in the quantitative collections. At that time the young crayfishes measured from 6 to 16 mm. cephalothorax length, and the juvenile population had become divided into two size groups (Graph 28), each with a distinct mode. These two groups, however, were not separated on the basis of sex, for each group contained individuals of both sexes.

At the time when it was first possible to differentiate between the sexes, the first abdominal appendages of all the males were of the "juvenile" form. The two rami of each first abdominal appendage in the young males at this time were perfectly straight and parallel and were relatively uniform in thickness from base to tip. At the same time the ends were blunt and rounded, showing no hint of a point. The rami of the first abdominal appendages of adult "second" form males always show a tendency to be thicker at the base than at the tip, and have ends which are bluntly pointed rather than rounded.

The question has never been raised as to whether or not the "second" form of adult males is the exact equivalent of the "juvenile" form of the immature males, which is likewise usually referred to as the "second" form. Creaser (1933) states definitely that the "second" form is a developmental stage. Most writers, Faxon (1884), Harris (1901 and 1903), and Creaser (1933), have assumed that the two forms are identical, and that at times other than the breeding season the first abdominal appendages of mature males revert to the immature or juvenile condition. In view of the slight but constant differences just pointed out, it seems more justifiable to consider that the "second" form of adult males is only a partial equivalent of the "juvenile" form of young males, and that the reversion of the copulatory appendages of adult males after the breeding season is only a partial reversion in the direction of the juvenile condition.

GROWTH OF THE JUVENILE POPULATION

Increasing Range of Size.—During the summer, the spread between the largest and smallest members of the juvenile population increases progressively. Whereas in the June 7th collection (Graph 26) this "spread" amounted to only 2 mm. cephalothorax length, it increased to 6 mm. in the June 25th collection (Graph 27); 10 mm. in the July 10th collection (Graph 28); 13 mm. in the July 22nd collection (Graph 29); and 15 mm. in the August 31st collection (Graph 31). Similarly in 1932, the "spread" increased from 9 mm. in the collection of June 29th (Graph 4) to 14 mm. in the collection of September 15th (Graph 8).

This spread gives conclusive evidence of the establishment of individual differences in growth rate, and since growth in crayfishes is

conditioned by the molting process, there is a definite tendency for the growing population to become segregated into distinct groups rather than to vary at random.

Number of Size Groups.—The juvenile population forms a single unimodal size group (Graph 26) when it first appears. With the operation of differentiating growth factors during the summer this population becomes first bimodal and later polymodal. In the summer of 1933 the bimodal condition appeared in the collection of July 10th (Graph 28), a little more than a month after the juvenile population first appeared in the collections. In 1932 the juvenile population was already bimodal when the first collection was taken on June 29th (Graph 4) at the beginning of the present study. In these two apparently corresponding collections there were two major modes, and also a few individuals in advance of the more advanced of these two modes, forming a minor mode of their own.

During the summer the two major modes tend more and more to break up (compare Graphs 4, 5, 6, 7, and 8 for 1932; and Graphs 28, 29, and 30 for 1933) until finally in the late summer the population becomes definitely polymodal (Graphs 8 and 30). In both of the years during which the study was carried on the juvenile population came to exhibit five major modes, indicating the presence of five major size groups, at the end of the summer.

The first appearance of these five size groups among the juvenile population in 1932 was in the collection of July 27th (Graph 6). However, in this collection there were still two major groups. These were accompanied by three minor ones. Two of these minor size groups were in advance of the more advanced of the two major groups, and one was still less advanced than the less advanced of the two major groups. On August 11th, however, the five size groups were all well defined (Graph 7), and by September 15th (Graph 8) all traces of the two major size groups of summer had disappeared.

In 1933 the five major size groups first appeared in the collection of August 5th (Graph 30), and from that time on they maintained their identity more or less faithfully throughout fall and winter.

Constancy of Size Groups.—In both the 1932 and the 1933 populations these size groups could be identified, usually very prominently, in nearly all collections after they had become established. Sometimes one of them was represented by a mode affecting one sex only, either male or female, but the writer found, as did Creaser (1934), that the males and females exhibited no appreciable differences in the length of the cephalothorax, and that modes affecting only one sex could safely be used for drawing conclusions regarding size groups. Usually a size group repre-

sented only by a male or by a female mode in one collection would occur strongly in both sexes in the following collection. The same was true in cases where one size group was absent altogether from a collection. This happened occasionally, but in every case one of the later collections, usually the one immediately following, would show the group as strongly present as ever, and with a mode in the same place, or approximately the same place, as it had appeared previously. This was true in the case of the usual collections of 60 or more individuals, and it proved to be equally true in the mid-winter collections when it was sometimes impossible to secure more than 30 individuals on a collecting trip. Even in these small collections the five size groups usually maintained their identity perfectly.

This experience, borne out by two full years of collecting, led the writer to abandon all doubt as to the validity of the method of study.

Significance of the Size Groups.—Most of the records regarding the growth rate of young crayfishes have been taken from observations of single individuals, or, at most, of small groups of individuals. All such records have been secured under laboratory conditions. Smith (1910-11) found that in fifteen individuals of *C. propinquus* which molted in the laboratory, the increase in cephalothorax length accompanying the molt was 2 mm. in all but four cases. In three of these four cases the increase was 3 mm., and in the other case it was 2.5 mm. Andrews (1904) in studying the young of *C. affinis* found the following body lengths for the growing young: first instar, 4 mm.; second instar, 4.5 mm.; third instar, 8 mm.; fourth instar, 12 mm.; fifth instar, 15-18 mm.; sixth instar, 21 mm.; seventh instar, 29 mm. The average of the differences between these sizes is 4.9 mm. This represents the average increase in total body length accompanying a single molt. This is equivalent to approximately 2.45 mm. cephalothorax length. Therefore in the young of *C. affinis* which were studied by Andrews, the average increase in cephalothorax length was approximately 2.45 mm. for each of the first six molts.

In the present study it was found that the average distance between the modal points, both in the bimodal and polymodal conditions was 2.42 mm. In the majority of cases the distance was 2 mm., but in some cases it was 3 mm. or 4 mm. The size groups among the juvenile population, as represented by the modes, in both the bimodal and polymodal conditions, consist of groups of individuals within the population which have maintained approximately the same growth rate. The differences in size between the modal groups represent the average growth increment of each group over the group of next smaller individuals. In the light of the observations of Smith and of Andrews, it appears that the difference in size between any group, and the group immediately smaller, represents the average increment resulting from a single molt. Therefore, if a group

is advanced in size by 2, 3, or more millimeters beyond the one immediately to its left on the population graph, it is because the individuals of the first size group have undergone one more molt than the individuals of the immediately lesser size group. During that molt the individuals of the more advanced size group made an average increase in cephalothorax length of 2 mm., or 3 mm., or whatever may be the distance between the particular two modes in question.

We may safely conclude, then, that the distances between the modal points represent the average growth increments of different size groups as the result of single molts. On this basis the average increment resulting from a single molt among the juvenile population during their first season was 2.42 mm.

Therefore, the bimodal condition (Graph 28) bespeaks a population a part of whose members have undergone one more molt than the smaller individuals in the population. The presence of a very few individuals advanced in size beyond the more advanced of the two major size groups (Graph 4) gives reason for believing that these few individuals have undergone two more molts than the smallest members of the population.

Similar reasoning applied to the polymodal condition, showing the five major size groups found in the population at the end of the summer, leads us to believe that the members of the most advanced of these groups have undergone four more molts than the members of the least advanced group.

Size at the End of the First Growing Season.—At the end of the first growing season the largest individuals of the season's young may have reached a cephalothorax length of as much as 27 mm.; while the smallest individuals may have reached a cephalothorax length of only 12 mm. In the fall of 1932 the members of the largest of the five size groups ranged from 24 to 27 mm. cephalothorax length while those of the smallest of the five groups ranged from 13 to 16 mm. In the fall of 1933 the largest ranged from 22 to 26 mm., while the smallest ranged from 12 to 15 mm. The generally smaller size of all individuals of the young population at the end of the 1933 growing season which is thus apparent is a further effect of the retarded spring season and late hatching of 1933.

Differences in Growth Rate During the First Season.—If the average growth increment as a result of each molt during the first growing season (after the first two molts which are presumed to have occurred before the young appeared in the quantitative collections) is 2.42 mm. then the approximate number of molts undergone during the first growing season may be ascertained by the following formula:

$$\frac{x-y}{2.42} + 2 = z$$

- x = mode of the size group in question at the end of the season.
 y = mode of the juvenile population when it first appears in the quantitative collections.
 2.42 = the approximate average growth increment with a single molt.
 2 = number of molts undergone by the young crayfishes before they appear in the quantitative collections.
 z = total number of molts undergone.

For greater accuracy, x should represent not simply the mode of the size group in question for a single collection taken at the end of the season, but rather the average of the extreme ranges which the mode of the group may occupy as ascertained by repeated collections taken at intervals over a considerable period after the growing season has ended. The mode of the first appearing juvenile population is used for y rather than the average for that population, because any expression of the average in round numbers would be identical with the mode.

Thus, in the case of the largest size group in the population at the end of the 1932 growing season (24 to 27 mm.):

$$x = 25.5$$

$y = 5$ (This is taken from the mode of the juvenile population when it first appeared in the quantitative collections on June 7, 1933. This number is probably a constant).

$$\text{Therefore: } \frac{25.5 - 5}{2.42} + 2 = \text{approximately } 10 = \text{total number of molts or } z.$$

In the case of the second size group from the right on the graph (the second most advanced), by similar calculation the number of molts undergone would be approximately 9. In the case of the third size group from the right (the third most advanced) it would be approximately 8. For the fourth size group it would be approximately 7, and for the fifth size group approximately 6.

Thus the young crayfishes which are hatched in May or June pass through 6 to 10 molts during the first growing season with an average increment of 2.42 mm. cephalothorax length (equivalent to approximately 5 mm. total body length) with each molt. By mid-September they measure 12 to 27 mm. cephalothorax length which is equivalent to approximately 24 to 54 mm. total body length.

Other writers on the group of the crayfishes have recorded similar differences in growth rate among the juvenile population. Andrews (1904) in his work with *C. affinis* noted wide differences in growth rate among the season's young. "During these 2 months and 3 weeks of summer," he says, "some few seem not to have grown at all, while about a third of them have almost doubled their length." Writing again in 1907 he estimates that the young of *C. affinis* pass through 11 to 13

instars during their first summer; but he says that in some cases the young crayfishes may be only 20 mm. long in the fall, due apparently to their development being arrested during the 6th instar. He gives the body lengths of 101 specimens of *C. affinis*, which he raised in laboratory aquaria, as being 20 to 62 mm. in the October following their first growing season.

Ortmann (1906) in his life history of *C. obscurus* says that the young crayfishes hatched in May or June measure 26 to 50 mm. body length by the end of September. He says: "It seems that the rate of growth of young crayfishes is very different in different individuals, some gaining through June, July, August, and September only about 15 mm. in length, others more than twice that length."

Creaser (1934) writing of *C. propinquus* in Michigan, says that the season's young attain a size of 10 to 20 mm. cephalothorax length by September. This is equivalent to a body length of 20 to 40 mm.

Thus in every case in which the growth of young crayfishes during the first season has been observed, it has been found that the rate of growth differs greatly among individuals and that therefore the spread between the largest and smallest individuals or groups in the population increases during the summer and reaches a climax in late September or early October at the close of the growing season.

Causes of the Differences in Growth Rate.—Although all students of the group of the crayfishes agree as to the remarkable differentiation in size which takes place during the first season among the originally homogeneous juvenile population, only Andrews (1907) attempts to account for it. He suggests that insufficient food may be the cause of the lack of growth on the part of the smaller individuals. In speaking of one brood of laboratory-reared crayfishes which averaged 50 mm. body length in the fall as against an average of 41 mm. for the entire group reared in the laboratory, he attributes the advanced size of this brood to its having had more food and possibly also more favorable conditions of temperature than the remainder of the group. In another connection he says, "the rate of growth was very different in individuals, and in some cases seemed to depend directly upon food supply."

Andrews' specimens were all carried through the first growing season in the laboratory, and the reasons which he gives for the retardation of the growth of a portion of them as compared to the rest are more applicable to laboratory-reared crayfish than they are to crayfish which grow up under natural conditions. In the natural environment temperature as a cause for retardation of growth is ruled out as all members of the juvenile population are subjected to approximately the same temperature conditions. Shortage of food is likewise not likely to affect any portion of the population except in abnormal seasons, since in the locality which

was studied by the writer, there was more than abundant food for all the crayfish there, both young and old.

It seems to the writer that the differences in rate of growth are more probably due to inherent genetic growth factors than simply to environmental causes. The environmental conditions undoubtedly influence the expression of these inherent genetic factors, however, and probably determine the upper limit of size which may be attained in a particular season. This was apparently the case in 1933, when the retarded spring season resulted in the attainment of a smaller total size in the case of all groups than in the preceding season of 1932.

ATTAINMENT OF SEXUAL MATURITY

Sexual Form of Males at the End of the First Season.—Until the end of the summer the males of the season's young remain in the juvenile form. During August and the first half of September, however, there is a progressive change from the juvenile condition to the first form. Table 3 shows the progressive change in form among the young males during the late summer and early fall of 1932.

TABLE 3.—PROGRESSIVE CHANGE OF FORM OF YOUNG MALES

Date of collection	Total number of young males	Number in juvenile form	Number in first form
Aug. 11, 1932.....	23	23	0
Sept. 15, 1932.....	14	8	6
Sept. 26, 1932.....	28	16	12
Oct. 6, 1932.....	51	8	43

After the beginning of October, in 1932, the first form males continued to outnumber the juvenile males among the season's young in most of the collections taken during the fall and winter. This condition of the juvenile population probably represents the normal fall and winter condition at this latitude.

In 1933 the results were less conclusive. In two collections taken during September and October (Sept. 20th and Oct. 7th) the first form males outnumbered the juvenile males among the young of the season. In the other fall and winter collections the number of juvenile males exceeded the number of first form males by a ratio which was in most cases approximately two to one. It seems probable that in the fall and winter of 1933 the number of juvenile males really exceeded the number of first form males among the season's young at all times, and that the two collections in which the opposite was true were the result of inaccurate sampling. Such a conclusion is in accord with the results of the

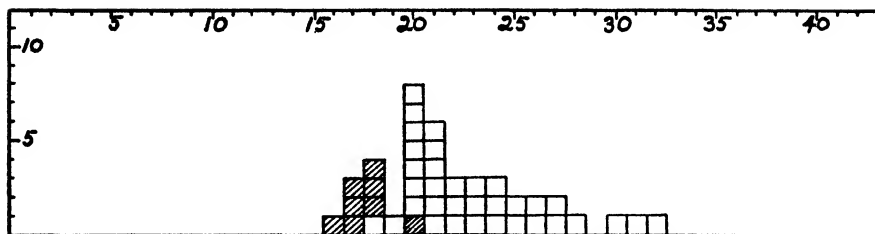
majority of the fall and winter collections of 1933-34, and also with the generally delayed appearance of all crayfish life history phenomena in the season of 1933.

A similar relation of the length of the growing season to the percentage of males of the young of the year which reach maturity by the first fall is evident in the work of Creaser (1933) and of Smith (1911) with *C. propinquus*. Creaser working with this species at Ann Arbor, Michigan, where the growing season is necessarily shorter than at Urbana, Illinois, found that some males of the season's young became first form by the beginning of fall, but that the great majority of them did not do so. Smith, in a collection taken at Douglas Lake, Michigan, on Aug. 5th found that among 16 young males, 4 were first form and 12 were still juvenile. In a collection recorded for the same day taken at Urbana there were 30 young males, 21 of which were first form and 9 juvenile. Thus in collections taken on the same day, the majority of the young males in the Michigan population were still juvenile, while the majority of those in the Illinois population had already become first form. Therefore, apparently the longer growing season characteristic of the more southern location not only enables a higher percentage of the young males to reach maturity by the end of their first growing season at Urbana, Illinois, than in central Michigan, but also causes the young of the Urbana population to show greater advancement at any particular time during the late summer.

Investigators working on other species of crayfish have likewise found that a portion of the young of the year reach maturity by the end of the first season. Ortmann (1906) in the study of the closely related species, *C. obscurus*, in Pennsylvania found that most males of the season's young become first form by October. With *C. affinis*, also, Andrews (1904) found that in Maryland a portion, at least, of the young males attain maturity by the beginning of the first fall after they are hatched.

Size of Males at Sexual Maturity.—It was found in the present study that a cephalothorax length of 20 mm. marked approximately the boundary between sexual maturity and immaturity among the males of less than one year. The individuals measuring 20 mm. and above were generally found to be first form, indicating that they had attained sexual maturity, while those that measured less than 20 mm. were generally immature. This division however was by no means absolute. Individuals which had reached sexual maturity below 20 mm. were not uncommon, and occasional individuals were found which had passed this size and were still immature.

The accompanying distribution curve (Graph 1) represents sexual maturity in males in a winter collection which was typical of the collections taken after the end of the growing season. The unshaded portions



GRAPH 1.—Showing the distribution of sexual maturity among the males in a typical winter collection (February 18, 1933). The shaded squares represent the immature, and the unshaded squares the mature individuals. The abscissa represents cephalothorax length in millimeters.

of the graph represent the mature males, and the shaded portions represent the immature males. In this graph the fact that an approximate boundary between maturity and immaturity exists at 20 mm. cephalothorax length is plainly apparent.

First form males below 18 mm. cephalothorax length were exceedingly rare, although one was taken on November 17, 1932, which was only 12.6 mm. The largest immature male taken measured 23.1 mm. cephalothorax length. This individual occurred in the collection of November 3, 1932. True second form males of a much larger size than this were found between the first and second adult molts of the adult males in the spring, but in the opinion of the writer a distinction may properly be made between the juvenile condition of the copulatory appendages, and the true second form condition as it occurs in adult males. Therefore these large second form males cannot be placed in the same class as the immature males.

The boundaries of sexual maturity among the males of *C. propinquus* which were indicated in the present study agree with those recorded for the same species by Smith (1910-11). In her work, as in that of the writer, 20 mm. cephalothorax length formed an approximate lower boundary for sexual maturity among the males. She found that the great majority of first form males measured 20 mm. or more, and she found no first form males at all below 17 mm.

Ortmann (1906) found a similar size limit in *C. obscurus*. He found that in this species a body length of 40 to 50 mm. (corresponding to a cephalothorax length of approximately 20 to 25 mm.) was indicative of sexual maturity among the males. The smallest first form male that he found measured 38 mm. body length (approximately 19 mm. cephalothorax length).

A slightly different result, however, was obtained by Creaser (1933) in his study of the *C. propinquus* of Michigan. If we may judge by his graphs, he found a much greater percentage of first form males measur-

ing below 20 mm. cephalothorax length than occurred in the studies of either Smith or the writer. Indeed, in his collections, the size of 20 mm. seems to be totally without the significance which it was found to have in the Illinois population. The size of 16 mm. or 17 mm. would apparently hold something of the same significance in Creaser's collections. This difference between the results of Creaser and those obtained by Smith and the writer for the Illinois population is largely explainable on the ground that Creaser's population represented a smaller race of *C. propinquus* than that found in eastern Illinois. This theory finds support in the fact that Creaser's largest adults rarely exceeded 30 mm. cephalothorax length, whereas in the race of crayfish used in the present study, a portion of the yearling adult group regularly exceeded 30 mm., and the absolute maximum of size seemed to be between 35 and 40 mm. Creaser's crayfish seem, therefore, to have averaged from 3 to 5 mm. smaller in cephalothorax length among all size classes than the Illinois crayfish.

Sizes of Females at Sexual Maturity.—There is no available criterion for determining whether or not individual females among the young of the year are sexually mature at the end of their first growing season. However, a general idea of the boundary of sexual maturity among the young females can be obtained by observing the sizes of the females seen in copulation during the fall. In the present study no females below a cephalothorax length of 20 mm. were found copulating, but apparently females of 20 to 25 mm. cephalothorax length (all young of the season) were quite as likely to be taken in copulation as were older and larger individuals.

Similar results were obtained by Smith (1910-11). She also found copulation taking place with females of as low as 20 mm. cephalothorax length, undoubtedly belonging to the young of the season. Likewise in the closely related species, *C. obscurus*, Ortmann (1906) observed copulation in the fall among the sexually mature individuals of the season's young, the smallest female taken in copulation having a body length of 43 mm. (approximately 21 mm. cephalothorax length).

A further and more general criterion for sexual maturity among the females is furnished by the size of the females found bearing eggs in the spring. The evidence from this source fully verifies the existence of an approximate lower limit of sexual maturity among the females at 20 mm. cephalothorax length. Thus apparently with females as with males, this size forms the approximate boundary of sexual maturity among the young of the year in the race of *C. propinquus* found in eastern Illinois.

COPULATION

In connection with the present study pairs of *C. propinquus* were taken copulating or in copulatory attitude in the months of September, October, November, and March. Smith (1910) found copulating crayfish of this species in the field at Urbana, Illinois, in October, November, and December; and at Douglas Lake, Michigan, in July and August. Hay (1919) found *C. propinquus* copulating in Lake Maxinkuckee, Indiana, in November, January, and April. Turner (1926) gives the date of September 1st in Michigan and August 25th in Wisconsin for the observation of copulation in *C. propinquus*. Creaser (1933) says that in the vicinity of Ann Arbor, Michigan, the mating season of the species is in October and November.

Thus it seems that the occurrence and duration of the mating season of *C. propinquus* varies widely with the locality. In more northern latitudes, such as Michigan and Wisconsin, it probably begins in July and August, and lasts until November, but does not occur again in the spring.

In more southern latitudes such as east-central Illinois and Indiana it probably begins in September and lasts until the onset of severe winter weather in December or January, then begins again in March, and may last into April. It is possible that with mild winter temperatures such as occur in some years, the mating season might last throughout the winter at the latitude of Urbana, because males will attempt to copulate at any time during the winter if warmed and placed in close confinement with females.

This corresponds to the experience of Pearse (1910) who found that male crayfish during the mating season will attempt copulation almost immediately if placed in close confinement with females, and also to the experience of Bell (1906), who found increased sexual activity among the males accompanying a rise in temperature.

In copulating pairs the male and female are usually approximately the same size, although occasionally the writer has seen larger males attempting to copulate with smaller females in laboratory aquaria. Creaser (1934) says: "Presumably only a small percentage of females can mate as young of the year, unless the males are polygamous, because observations indicate that mating pairs are of about the same size." The writer during two years of observation saw nothing to indicate that male crayfish are necessarily monogamous, and Andrews (1895) says definitely that in *C. affinis* conjugation may be repeated by either animal with some other individual.

STATIC CONDITION DURING THE FALL AND WINTER

After the latter part of September or the early part of October growth ceases in all cases. In the present study the latest date at which a "soft," freshly molted individual was taken was October 6th. This individual was a young female and measured 17.1 mm. cephalothorax length.

In the collections taken during the fall and winter the five size groups in the population of the young of the year remain distinct and maintain relatively constant levels of size. In the different collections the mode of each group may vary back and forth within a range of 2 to 4 mm., but in all cases the five modes representing the five size groups maintain the same general relations to one another (Graph 3).

The variation in the position of each mode is indicative of the operation of two factors: (1) the individual variation among the members of each size group, and (2) the vagaries of sampling. Consistently larger collections might have produced less variable results.

Other investigators have likewise found a cessation of growth in the early fall, and a static condition of the population during the fall, winter, and early spring. Andrews (1907) says of *C. affinis*: "After October there are no more molts until the following warm season, the lengths remaining constant through the winter." Ortmann (1906) says that in *C. obscurus* the winter is passed without change. According to Creaser (1934) there is no growth among the *C. propinquus* of Michigan after about September 24th. And Turner (1926) writing of crayfish in general says: "During the winter, growth . . . is at a low ebb, and no molting takes place."

In all cases this absence of molting may be easily seen from the condition of the exoskeleton. In all crayfish, large and small, taken in the winter collections, the shell is dark, almost black, and is frequently covered with algal and protozoan growths.

Creaser (1934) advanced the theory that the cessation of growth and molting in the early fall might be caused by falling temperature, and he related this to the fact that at Ann Arbor, Michigan, he observed no crayfish feeding during the winter months. It seems probable that the phenomenon may be related to falling temperature, although in 1933, at Urbana, during the period in which the cessation of growth was noticed the days were still warm, with temperatures ranging from 15° to 20° Centigrade. The temperature control, however, if such it is, must operate in some way other than to cause the crayfish to stop eating, for the writer found food in the process of digestion in the stomachs of *C. propinquus* taken in December. Furthermore, the crayfish are relatively active for six weeks after growth has ceased in the fall, and Hay (1919) reports seeing

crayfish of this species feeding regularly during October and the first half of November in Lake Maxinkuckee, Indiana.

It seems likely that the gradual lowering of the mean temperature for the 24-hour period which takes place during the early fall, largely on the account of the occurrence of cooler nights, may cause a slowing of the physiological processes of the animals to a level of mere maintenance, thereby bringing about a cessation of growth and molting.

This seems particularly probable in view of the fact that recent studies such as that of Markus (1933) on the relation of temperature to the rate of digestion in the black bass, have shown that in cold blooded forms a very close correlation exists between temperature and the rates of physiological processes.

SPRING REPRODUCTIVE ACTIVITIES

Kinds of Activity.—Except for the occurrence of copulation in the spring in some localities the reproductive activities of spring concern the females only. They consist of two distinct phases: (1) the laying and carrying of the eggs, and (2) the hatching and carrying of the young.

It was necessary to treat fully the second phase of the female reproductive activities, that is, the hatching and carrying of the young, at the beginning of this study, in connection with the appearance of the first young of the season. The first phase of these activities, however, the laying and carrying of the eggs, although it was necessarily mentioned in connection with the hatching of the young, is more properly considered at this point in the description of the life cycle, since it is directly related to all of the events which take place among the adult female group at this time.

Egg Laying.—During a part of the month of March the adult females are largely absent from the active population. Table 4 shows the ratio of males to females for two typical winter-time collections, two collections taken during the month of March, 1933, and two taken during the month of April, 1933. The purpose of the inclusion of the two winter collections in the table is to show the normal sex ratio as a basis for comparison

TABLE 4.—SEX RATIO IN WINTER AND SPRING COLLECTIONS

Date of collection	Males	Females	Percent males	Percent females
Jan. 26, 1933.....	35	24	60	40
Feb. 18, 1933.....	42	33	56	44
Mar. 4, 1933.....	56	20	74	26
Mar. 18, 1933.....	51	15	77	23
Apr. 8, 1933.....	29	22	57	43
Apr. 22, 1933.....	32	29	52	48

with the March collections when the females were largely absent, and the April collections when they have rejoined the active population.

From Table 4 it is seen that the males outnumber the females normally to a slight extent. This ratio in favor of the males, however, markedly increases during the month of March, and returns to normal shortly after the beginning of April.

The first females bearing eggs appear coincident with the return of the adult females to the active population in early April. In 1933 the first egg-bearing females were taken in the collection of April 8th. In 1934 they appeared in the collection of April 7th.

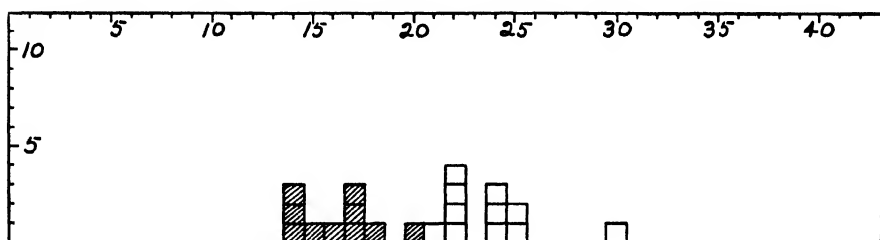
High water handicapped the work of collecting during the month of March in both years, so that a proper search for the missing females could not be made. However, since most of them reappear in early April, bearing eggs, it may be reasonably assumed that their absence during March is connected with the laying of the eggs. Andrews (1895 and 1904) tells of the extreme excitability of the females of *C. affinis* as egg-laying time approaches. It is reasonable to suppose, then, that during the egg-laying period and for some time prior to it the females remain hidden and inactive. Therefore, we reasonably may consider that the eggs in *C. propinquus* are laid in late March or early April, and that most of them are laid at about the same time, since the disappearance and reappearance of the females takes place *en masse*. One female, however, of sexually mature size was found without eggs on April 22, 1933, and on examination it was discovered that a normal clutch of well-developed eggs were still internal, having not yet been laid. Whether this female would have laid later, or whether she would have produced young at all, cannot be determined. However, no young were found in either 1932 or 1933 which bore evidence of belonging to so late a hatch as this would have been.

The conclusion that the eggs of *C. propinquus* are laid in late March or early April at Urbana, Illinois, corresponds closely to the results of Smith (1910-11) for this species in the same location, and also to the results of Ortmann (1906) for the related species *C. obscurus* in Pennsylvania. Smith found the first females with eggs on March 25th. Ortmann found no egg-bearing females on March 28th or March 31st, but found numerous ones on April 6th. In the work of these investigators, as in that of the writer, the eggs apparently were laid in almost all cases at practically the same time.

Egg Carrying.—During the two years of the present study, females bearing eggs were taken only during the months of April and May. Egg-bearing females were present in the collections of April 8th, April 22nd, May 6th, and May 21st, 1933; and of April 7th, April 28th, and May 5th,

1934. After the initial appearance of egg-bearing females practically all sexually mature females were found with eggs.

These results again agree closely with those obtained by other investigators. Smith (1910-11) found practically all sexually mature females of *C. propinquus* carrying eggs on April 29th, and collected the last egg-bearing female on May 18th. Pearse (1910) took *C. propinquus* females with eggs at Walnut Lake, Oakland County, Michigan, on May 2nd, and June 6th; at Coldwater, Michigan, on April 17th; and at Ann Arbor on April 18th. Creaser records 15 females of this species as being taken with eggs near Dexter, Michigan, on May 24th.



GRAPH 2.—Showing the distribution of egg-carrying among the females taken in the collection of April 8, 1933. The shaded squares represent females not carrying eggs and the unshaded squares those carrying eggs. The abscissa represents cephalothorax length in millimeters.

Thus the egg-bearing season for *C. propinquus* apparently lasts during the month of April and a part or all of the month of May in the latitude of Urbana, Illinois, and probably lasts from mid-April to early June in the more northern latitude of Michigan.

Size of Females Carrying Eggs.—The lower size limit of the females bearing eggs corresponds to the general lower size limit of sexual maturity among both males and females, as ascertained at the time of copulation in the fall. Here again the cephalothorax length of 20 mm. forms an approximate boundary, separating, in this case, those females which bear eggs from those which do not.

In the accompanying graph (Graph 2) of the female population taken in the collection of April 8, 1933, during the egg-bearing season, this boundary is clearly evident. The shaded portions of the graph represent those females which were not carrying eggs at the time the collection was made. The white portions represent the egg-bearing females. This graph represents the condition of the female population typical of the egg-bearing season.

The occurrence of females below 20 mm. cephalothorax length with eggs was rare. Such females were taken occasionally, however. The

smallest female found with eggs measured 16.1 mm. cephalothorax length, and was taken on May 6, 1933. The largest female taken without eggs during the egg-bearing season measured 24.9 mm. cephalothorax length and occurred in the collection of April 28, 1934.

Smith (1910-11) obtained results with *C. propinquus* similar to those of the present study. She found no egg-bearing females measuring less than 18 mm. cephalothorax length. Likewise, Ortmann (1906) found 40 mm. body length (approximately 20 mm. cephalothorax length) to be the lower size limit of egg-bearing among females of *C. affinis*.

Creaser (1934), however, obtained somewhat different results with the Michigan race of *C. propinquus*. He records the cephalothorax lengths of 14 egg-bearing females as follows: "one each, 15, 16, 17 and 18 mm.; five 19 mm.; and one each: 20, 21, 23, 24 and 25 mm." Here the size boundary of 20 mm. cephalothorax length appears to be without significance. This is in accord with the results which he obtained concerning the size of the young males at the time of attainment of sexual maturity, and it may likewise be explained by assuming that Creaser was working with a generally smaller race of *C. propinquus* than that occurring at Urbana, Illinois.

Number of Eggs Carried by the Females.—The numbers of eggs carried by the females were found to be roughly proportional to the sizes of the individuals. The largest female taken with eggs measured 36.1 mm. cephalothorax length and had an estimated clutch of 175 eggs. The largest clutch, estimated at 250 eggs, was borne by a female measuring 31.4 mm. cephalothorax length. The smallest female which was found bearing eggs measured 16.1 mm. cephalothorax length and had an estimated clutch of 40 eggs. The smallest number of eggs found on any female was 5, and occurred on a female measuring 21.7 mm. cephalothorax length. In this case, however, as in a number of other cases showing only a few eggs, the manner in which the eggs were scattered on the pleopods gave evidence that the few eggs were only the remains of a larger clutch, the majority of which had been lost.

Smith (1910-11) records additional evidence which shows that the number of eggs carried is in general proportional to the size of the individual female. She found a female measuring 38 mm. cephalothorax length which was carrying 225 eggs, and another measuring 20 mm. cephalothorax length, and carrying 102 eggs. These cases agree essentially with the results obtained in the present study.

SPRING MOLTS OF THE YEARLING GROUP

Criterion for Determining the Occurrence of First Molts.—The collector has no difficulty in determining which individuals among the cray-

fish taken in the spring collections have undergone a molt and which have not done so. Up to the time of their first molt in the spring the shells of all of the crayfishes of both sexes, whether large or small, retain the dark color characteristic of the winter season. They frequently retain also the encrusted algal and protozoan growths which accumulate during the winter.

Number of Molts Among the Mature Yearling Males.—There have been various observations recorded by a number of investigators concerning the number of molts undergone by male crayfishes during the second season after they are hatched. In most species which have what Ortmann (1906) called the "warm water type" of life history, it has been found that the adult males undergo two molts during their second season. The first of these has been generally called the "spring" molt, while the second molt has been variously called the "summer" or "fall" molt, depending on the time of its occurrence. It will be shown in this study that during one of the years in which the investigation was carried on, this second molt of the adult males occurred so early in the season that it did not even justify the use of the term "summer" molt. Therefore it has seemed best in the present study to refer to these molts as the first and second adult molts of the males.

Both of these molts involve changes of the form of the first abdominal appendages on the part of the adult males. These males have passed through the winter with first abdominal appendages of the first form. They become second form as a result of the first adult molt and then revert back to first form as a result of the second adult molt.

The First Adult Molt of the Mature Yearling Males.—The first molts among the adult males in the spring appear in April or May. In 1933 the first newly molted males of this group appeared in the collection of May 6th. Out of 21 adult males taken on that day 5 were newly molted. In 1934, however, the first newly molted adult males appeared in the collection of April 7th, along with the first egg-bearing females. At that time, out of 63 adult males, 22 were molted.

It seems probable that the occurrence of the first adult molt in 1934 was more nearly normal than that in 1933, since the laying of the eggs by the females, and the new molts of the males represent correspondingly initial spring activities on the part of the two sexes. Also, it is well to remember again in this connection that the spring of 1933 was very much retarded while the spring of 1934 was relatively normal.

The first adult male molt occupies a relatively short period of time. In 1933 the first molted individuals of this group were discovered on May 6th and at the time of the next collection on May 21st all adult males were molted. In 1934 the first newly molted adult males were taken on

April 7th, and before the time of the next collection on April 28th, all had completed the molt.

Smith (1910-11) gives a slightly later date for the occurrence of the first adult male molt in *C. propinquus* than was recorded during either of the years of this study. She gives the date for its occurrence as being from May 13th to June 2nd. However, in view of the wide divergence found in the time of the occurrence of this molt as between the two years of the present study, this still later period given by Smith may easily be accounted for by the particular character of the season during which she worked.

Workers on other species of crayfish have obtained results similar to those obtained by Smith and by the writer for *C. propinquus*. Steele (1902) places the first adult molt for the males of *C. virilis* in Missouri from early April to mid-May. Ortmann (1906) says that with *C. obscurus* in Pennsylvania the first adult molt of the males takes place in most individuals during the first half of May, but that some individuals may begin as early as March.

In both *C. virilis* and *C. obscurus*, therefore, as well as in *C. propinquus*, the first adult male molt in the spring in most cases is accomplished sometime during the months of April or May. Undoubtedly in the case of a species like *C. propinquus* which occurs over a wide territory this molt takes place at a relatively later date in the more northern locations. And in all cases the earliness or lateness of the occurrence of the molt in any particular area is certainly dependent on the character of the season.

Second Adult Molt of the Mature Yearling Males.—After the completion of the first adult male molt in the spring there are no first form males in the population, since all of the males which had previously been first form became second form at the time of the first adult molt. Any first form males which occur in the late spring or early summer, therefore, are those which have also completed the second adult molt, since it is by this molt that the adult males again become first form.

In the writer's study of *C. propinquus* in 1932, a collection taken on June 29th showed 11 first form males and 9 second form males. Since these first form males had unquestionably completed the second adult molt it is evident that this molt was well advanced at that time. In the next collection, taken on July 14th, 4 first form males were taken, and one second form male. In all later collections taken during the summer all adult males were first form. It seems justifiable to conclude, therefore, that in 1932 the second adult male molt began in the latter part of June and was completed in nearly all cases by the middle of July.

In 1934 the second adult molt of the males was apparently a "second spring molt" rather than a "summer molt." On April 7th, 41 first form

males (still retaining their old winter shells) were taken along with 22 second form (newly molted) males. These second form males were all adult in size and had become second form with the first adult molt of spring. Apparently therefore, this collection was taken just in the middle of the first adult molt of the season. At the time of the next collection, taken on April 28th, all the adult males had lost their old winter shells, indicating that they had all passed through the first adult molt, and 7 out of 38 had also passed through the second adult molt, and become first form again. The remaining 31 males were still second form. Just one week later, on May 5th, only 7 males out of a total of 62 remained second form, all others had completed their second adult molt and become first form.

Thus apparently in the season of 1934, both first and second adult molts took place within a little more than a month among most of the adult male group of the population. Presumably at some time during the month of April, there was a short period during which all adult males were second form. Then, just before the collection of April 28th the second adult molt began, and it was largely completed by May 5th, just one week later.

It seems probable that the remaining second form males which had not yet undergone the second adult molt by May 5th did so during the remainder of May or in the early part of June. The second form males present in the collections of June 29th and July 14th, in the summer of 1932 probably represented such "stragglers" which underwent the second adult molt and changed to first form somewhat later than the majority of the adult male group.

Smith (1910-11) was unable to find evidence of any second adult molt at all among the males of *C. propinquus* in the Urbana population. This may now be explained on the basis that in the spring of 1911, as in that of 1934, the two molts occurred very close together. If this were true, she might easily have confused the two, and thought them a single extended molting period.

Apparently the occurrence of the second adult male molt among the *C. propinquus* of Michigan is more delayed, judging from the work of Creaser (1933) and of Smith (1910-11). Creaser's graph for a population sample taken on July 30th indicates that the second adult molt was largely finished by that time, since the adult males taken were mostly first form. These had mostly been second form in his graph for June 29th, showing that at that time the first adult molt had occurred but not the second. Smith found that all adult males were still second form at Douglas Lake, Michigan, on July 6th. On August 5th only one second form male of adult size was found, all the others having reverted to first form. Thus, in Michigan the second adult molt of the males must occur during July and early August.

Investigations on other species of crayfish have generally demonstrated that the second adult male molt occurs in summer rather than in spring. Steele (1902) says that this molt occurs among the *C. virilis* of Missouri between June 10th and July 1st with most individuals. Ortmann (1906) found that the second molting season for adult males began in July and lasted until late September, or early October, among the Pennsylvania population of *C. obscurus*.

The occurrence of the second adult molt of the males at so early a date as that recorded in the spring of 1934 for *C. propinquus*, at Urbana, has never been established for any other species of crayfish. It is impossible to say whether or not such an early occurrence of this molt is normal with this species at this latitude. It seems probable, however, that the second adult molt among *C. propinquus* may occur early in this way, whenever the season is sufficiently favorable.

Molting Among the Immature Yearling Group.—Those individuals among the previous year's generation of young which failed to attain sexual maturity by the end of the first growing season and which passed through the winter and spring in the immature state undergo their first yearling molt at the same time as the first adult molt of the males. Two females and one male of immature size were found newly molted along with the newly molted adult males on May 6, 1933. They also undergo a second yearling molt at the same time as the second adult molt of the males.

With the first yearling molt the immature males do not change the form of the copulatory appendages, but retain the juvenile form. With the second yearling molt, however, these immature males attain sexual maturity and become first form. Therefore, after this molt all yearling males in the population are first form. Presumably the immature females also become mature with this second yearling molt since they attain adult size as a result of it.

There is evidence that the members of this immature group also undergo a third and a fourth yearling molt during the summer.

This is in accord with the statement of Creaser (1933) who says: "Between March 17th and June 29th the young of the previous year resume their growth, rapidly increasing to adult size, probably by reason of several moltings." Creaser's "young of the previous year" were for the most part immature during the fall and winter, so their behavior would in general parallel that of the immature section of the previous season's young in the present study.

The Spring Molt of the Adult Females.—The adult females which have borne eggs during the spring, undergo only a single molt. This takes place immediately after the young are shed. In 1933 the first newly

molted adult females were found on May 21st. At the time of the following collection, taken on June 7th, the entire adult female population had molted. In 1934 the first newly molted adult females were found in the collection of May 5th, and in the following collection, taken on May 13th, all were molted.

Smith (1910-11) obtained similar results. She secured the first molted adult females on June 2nd, and found that the entire adult female group had completed its molt by June 6th.

GROWTH AMONG THE YEARLING GROUP

Growth Among Mature Yearling Males and Immature Individuals.—Since the first and second yearling molts of the immature group occur at the same time as the first and second adult molts of the yearling males, these groups may be considered together in the matter of growth during the two molts. In both years of the present study there was apparently no growth among either the adult yearling males or the immature group as a result of the first molt. Examination of the composite graph (Graph 3) shows that the lines representing all size groups, both mature and immature, remain essentially level during and following the time of this molt.

In contrast to the result of the first molt, the second molt of the adult males and immature individuals results in marked growth among both groups. The growth increment accompanying this molt varies from 3 mm. cephalothorax length in some individuals to as much as 8 mm. in others. The variation among individuals as to the amount of growth which accompanies this single molt stands in marked contrast to the condition prevailing during the juvenile growth period of the first growing season. Among the juvenile population differences in size apparently come about for the most part as a result of differences in the number of molts undergone rather than as differences in the amount of growth increment following a single molt. The distinctness of the size groups which were formed in the late summer among the juvenile population as a result of the differences in the number of molts undergone by different groups of individuals depended upon the fact that the individuals within each group had not only passed through the same number of molts, but had also undergone approximately the same amount of growth at the time of each molt.

As a result of the wide individual variation in growth rate in the spring at the time of the second yearling molt, there is a tendency for individuals to "migrate" into other size groups more advanced than their own, thus bringing about a "piling up" of individuals in the more advanced size groups at the expense of the less advanced ones. (Compare Graphs 25 and 26 for 1933, and Graphs 45 and 46 for 1934.)

The fact that the growth increment accompanying this molt was as much as 8 mm. cephalothorax length in some cases, while it was never more than half this much in the case of the juvenile molts of the first season is very interesting in view of the fact that there was apparently no growth at all in connection with the first yearling molt. Presumably the approximately doubled growth which takes place in some individuals at the time of the second yearling molt compensates for the absence of growth at the time of the first yearling molt.

The only published reference to the occurrence of a molt without growth in any species of crayfish is that recorded by Creaser (1933). He mentions the possibility that young males, at the end of their first growing season in the autumn, may molt without increase in size in case they undergo a change from the juvenile condition to the first form during the molt. In the present study, however, the molt without growth occurred in the spring and involved: (1) mature first form males which underwent a change to second form at the time; (2) juvenile males which remained in the juvenile form after the molt; and (3) immature females. Therefore, the case is in no way parallel to the one given by Creaser.

No full explanation of the absence of growth in connection with the first molt of spring can be offered at the present time. However, a consideration of the nature of the growth process in crayfish suggests a possible explanation. Since growth among crayfish is periodic, the anabolic processes between molts result in the accumulation of substances which are stored in the body as additions to the protoplasmic content and as stored food; but because of the physical limitations imposed by the integument the body does not increase in size until the confining shell is cast off. Then chiefly through imbibition of water the newly molted individual increases in size, reestablishing temporarily the equilibrium between formed substances and water content of the body. It seems probable that in the late winter and early spring physiological activity is reduced to a minimum because of the low temperature of the water. Under such conditions there would be no appreciable accumulation of substances. Therefore at ecdysis the imbibition of water would be negligible, and consequently with the first molt of spring there would be no appreciable change in size. Such an explanation seems particularly plausible in view of the fact that a correlation between temperature and physiological activity is probably the cause of the cessation of growth and molting among the crayfish population in the fall.

The third and fourth yearling molts of the immature group apparently result in about the same growth increment as was found to be characteristic of the juvenile molts (2 to 4 mm. cephalothorax length). These

two molts, however, and the growth accompanying them will be considered further in connection with the accounts of their occurrence.

Growth Among the Mature Females.—The second yearling molt of the adult males and the immature individuals occurs at approximately the same time as the single molt of the adult females. This molt involves growth among the adult female population of the same general extent and character as that which takes place in connection with the second yearling molt of the other two classes.

Thus the major portion of the growth among the yearling population takes place at approximately the same time in both sexes and in all size groups, although the molt by which it is accomplished among the adult females does not correspond to the one by which it is accomplished among the members of the other two classes.

ATTAINMENT OF MAXIMUM SIZE

As a result of the growth occurring in connection with the second yearling molt of the adult males and the single molt of the adult females, the entire yearling adult population reaches a size of 25 to 35 mm. cephalothorax length (Graphs 26 and 46). At the same time the size groups which were immature during the winter and spring attain a cephalothorax length approximating or exceeding 20 mm. (Graphs 26 and 46) and become sexually mature.

The 25 to 35 mm. cephalothorax length seems to constitute for the great majority of the race the maximum size which an individual may attain. During two years of observation and collecting, a small number of *C. propinquus* were taken which measured more than 35 mm. cephalothorax length. These individuals apparently represented special cases of survival and growth beyond the ordinary maximum size characteristic of the race. On June 29, 1932, a single male was taken which measured 40 mm. cephalothorax length. This was the largest individual ever found, and apparently represented the extreme upper limit of size for the race of *C. propinquus* occurring at Urbana, Illinois.

DEATH OF THE YEARLING ADULTS

Almost immediately following the second adult molt of the yearling males and the single molt of the adult yearling females, resulting in the attainment of the ordinary maximum size by these classes, the major portion of this adult population of both sexes completely disappears. In the collections taken after the middle of June, members of the maximum size groups are almost wholly lacking.

There remain three classes of individuals in the collections taken in

late June and early July (Graphs 27 and 28): (1) the young of the season, most of which are still below 12 mm. cephalothorax length; (2) a small adult group, measuring about 23 to 30 mm. cephalothorax length; and (3) occasional individuals measuring from 35 to 40 mm.

Apparently all or nearly all of the individuals of both sexes which were sexually mature during the winter and spring, and which produced the year's generation of young, die following the molt by which they attain maximum size. This phenomenon is clearly shown in the graphs representing the collections for June 7th and June 25th, 1933 (Graphs 26 and 27). In the collection of June 7th the adults of the winter and spring are still present in the population, measuring from about 25 to 35 mm. cephalothorax length. The immature individuals of the winter and spring, which now have become adult, all measure 19 mm. or more, and these, because of greater individual growth in a large number of cases, show a tendency to "pile up" on the adult population, thus shortening the range of the yearling group as a whole.

In the following collection, taken June 25th, the large adults are entirely absent, and the major portion of the entire yearling group has disappeared. There remain, besides the young of the season, only a few adult individuals which measure from 23 to 30 mm. cephalothorax length.

This condition continues relatively the same during the remainder of the summer. At no subsequent time does the large adult group reappear in the samples, as would be the case if they had gone into burrows or had migrated to other parts of the stream. Furthermore, a careful search made in holes in the bank along the water edge and in other parts of the stream revealed none of them.

Therefore we cannot escape the conclusion that, in the season of 1933, between June 7th and June 25th, most of the large adults died, including the major portion of the entire adult population, and that portion which produced most of the season's generation of young. The small adult group in the collection of June 25th, which ranges from 23 to 30 mm. cephalothorax length, apparently represents a portion, at least, of the group of individuals which passed through the winter and spring in the immature condition, and only became mature following their second molt in the spring. These individuals have apparently passed through a third molt, involving an increase in size of about 4 mm. cephalothorax length, between June 7th and June 25th, since on June 7th the smallest of them measured 19 mm. while on June 25th the smallest of them measured 23 mm. Definite evidence for the occurrence of this molt was found in connection with the collection of June 25th. In this collection two "soft," freshly molted females were taken which measured 25.4 and 28.3 mm. cephalothorax length, and which therefore belonged to the surviving yearling group.

PROBABLE NATURE OF ADULT DEATH

In the habitat under consideration *C. propinquus* plays a relatively important rôle in food chains. Fishes are the most important natural enemies of this species. During the present study no attempt was made to evaluate the effects of predators on the crayfish population. The progressive changes which take place in the crayfish population as the season advances, however, give no evidence of marked alteration attributable to the action of predatory species. Therefore it seems probable that the toll exacted by predators is a fairly uniform one, being relatively the same at all seasons, and affecting all classes of the population equally.

The death which decimated the adult population was undoubtedly a natural death, since no observed catastrophe took place which would account for it; and the fact that it affected only one class of the population precludes the possibility of its having occurred as a result of disease. Furthermore, it was not peculiar to the season of 1933, since a similar event had apparently taken place in 1932 before the first collection was taken on June 29th, judging from the size of the adult group in the four summer collections of 1932 (Graphs 4, 5, 6, and 7).

The occurrence of natural death in this species cannot be laid to the attainment of the ordinary maximum size alone, because the members of the small, remaining, yearling adult group, which measure from 23 to 30 mm. cephalothorax length in June, all attain the ordinary maximum size later in the summer, and survive at this size through the fall, winter, and the following spring. Therefore there must be some other factor which, occurring in conjunction with maximum size, acts as a contributing cause in bringing about natural death. Since natural death apparently involves only those individuals which have not only attained the ordinary maximum size, but which have also contributed to the production of the season's young, the coincident occurrence of parenthood and maximum size offers the basis for the most plausible theory regarding the immediately contributing factors which bring about their death.

The occurrence of natural death among adult crayfishes of maximum size coincident with the close of the reproductive season has been recorded previously by four different investigators. Creaser (1933) found natural death occurring among the adult males of *C. propinquus* in Michigan after the breeding season. Chidester (1912) likewise mentions the death of adult males after the breeding season in *C. bartonius bartoni*. He says that "in the spring the males die off in great numbers." Andrews (1904), writing of *C. affinis* in captivity, says: "After sexual union many died, and it was found that the males died in larger numbers than the females." Ortmann (1906) says concerning *C. obscurus*: "Another remarkable fact is that after the end of the molting season in spring no

very large males are found." He believes that the large males die, and describes in detail two cases in which he found males of the maximum size in a dying condition and yet bearing no injury of any kind. He believes it probable that the old females die in the same manner as the males, since they are entirely absent from the population after the young are shed at the beginning of summer.

The records of these investigators apparently bespeak conditions which were at least partially parallel to those found by the writer. The observations of Ortmann, in particular, afford an interesting comparison with the results of the present study, in view of the fact that *C. obscurus* and *C. propinquus* are closely related species. The fact that all four investigators found natural death occurring particularly among the males, parallels the fact that the writer found a marked excess of females among the small group of "oversize" individuals measuring from 35 to 40 mm. cephalothorax length. This is especially notable in view of the fact that in the population as a whole there was a definite preponderance of males.

THE SUMMER ADULT GROUP

The small group of individuals which survived the decimation of the adult population and which measured from 23 to 30 mm. cephalothorax length in the collection of June 25th (Graph 27) are represented regularly in the summer collections. These individuals were apparently those members of the yearling group which passed through the fall, winter, and spring in the immature condition, and which attained adulthood only at the time of their second yearling molt. Therefore they did not contribute to the production of the season's brood of young. They molted twice at the time of the first and second adult molts of the mature males in the spring and apparently molted again during the month of June.

By the early part of August these individuals have all attained the ordinary maximum size of 25 to 35 mm. cephalothorax length. Therefore they evidently undergo a fourth molt during late July or early August, involving a growth of 2 to 4 mm. cephalothorax length. Evidence for the occurrence of this fourth molt was obtained in two cases during the present study. The writer collected two "soft," freshly molted females, measuring 25.3 and 28 mm. cephalothorax length, on July 27, 1932. And in a collection taken for the writer on August 5, 1933, another "soft" female was taken, which measured 28.5 mm. cephalothorax length. All three of the individuals in question belonged to the yearling adult group.

This group, therefore, enters the fall at the ordinary maximum size, and lives at this size through the winter and spring. The individuals belonging to the group copulate in the fall, along with the mature members of the season's generation of young. The females of the group bear

eggs in the spring and produce young. Creaser (1933) expressed the opinion that the two-year-old males in the population of *C. propinquus* which he studied did not change into second form. In the Illinois population, however, the two-year-old males undergo the two spring molts along with the adult yearlings, changing to second form with the first spring molt and reverting to first form with the second. The females likewise undergo the single spring molt along with the adult yearling females. Most individuals of both sexes among the two-year-old group apparently undergo an increase of 2 mm. or more in cephalothorax length in connection with the second adult male molt and the adult female molt (Graphs 26 and 46). This gives to all of the individuals of this group a cephalothorax length of more than 30 mm., and to some of them more than 35 mm. Thus a portion of the group come to exceed the ordinary maximum size characteristic of the race.

Following these molts most of the individuals of this group die, along with the yearling individuals which have attained the ordinary maximum size and produced young. A very few of them, however, apparently survive and furnish the occasional "oversize" individuals, measuring 35 to 40 mm. cephalothorax length, which occur scatteringly in the collections throughout the year. At this size they apparently may survive through a third summer, fall, and winter, and escape natural death until the end of their third spring. During the two years of the present study only 34 individuals of this extreme size were taken, 21 of which were females and 13 were males. This unbalanced sex ratio apparently indicates that, among the two-year-old group at least, the factors which bring about natural death are more potent among males than among females.

This establishing of a differential death rate, leading to an elimination of males at an age earlier than that established for females of the same species, is in direct accord with the discovery of Van Cleave and Lederer (1932) who found that males of the snail *Viviparus contectoides* normally die shortly after reaching one year of age, while females normally attain the age of two years, and a few pass beyond the three-year limit.

AGE ATTAINED BY DIFFERENT GROUPS AND NUMBER OF BROODS PRODUCED

On the basis of the evidence drawn from the present study we may conclude that the majority of the *C. propinquus* in the Illinois population produce a single brood of young and die as yearlings. This holds true for those individuals which grow rapidly and reach sexual maturity by the end of their first growing season.

Those which fail to reach sexual maturity by the first fall after they are hatched, pass through the winter in an immature state and reach sexual maturity at the beginning of their second summer. They survive

through the second year and, after producing a single brood of young in their second spring, most of them die as two-year-olds.

A very few individuals, however, among which the females greatly outnumber the males, survive through a third year and die at the end of their third spring. It was impossible to ascertain whether or not these individuals produced more than one brood of young during their lives. The members of this size class copulated in the fall, and the females were taken with eggs in the spring, so that they were certainly fertile. There is a possibility, however, that this class may consist of individuals which were immature during their first year, and failed to produce a brood during their second year, thus not bearing their single brood of young until the spring of their third year. If this is true, then the individuals of this species never produce more than a single brood of young, and die soon after it is liberated. If the 35 to 40 mm. individuals form an exception to this rule it still remains true for the great majority of the race.

The common impression among most writers has been that all crayfish live normally to an age of three years or more. Andrews (1907) kept some *C. affinis* which had been hatched in the laboratory until they were more than three years old, and he believed that some very large individuals of this species found in the field might be six or seven years old. Ortmann (1906), after extensive field study of *C. obscurus*, concluded that the normal life span of the individual in this species was about three years. Turner (1926) on the basis of these studies gave four years as the approximate life span of crayfish in general.

The results obtained by Creaser (1934), however, on *C. propinquus* form a conspicuous exception to the conclusions of these earlier workers and agree very well with the results of the present study when due allowance has been made for the shorter growing season occurring in Michigan, where Creaser worked, as compared to Illinois where the present study was conducted.

Creaser found that most of the season's young in the Michigan population failed to become mature by the first fall after they were hatched, and that most of the yearling individuals survived into the second year. The majority of the yearling group in the Michigan population, being immature, corresponds to the small yearling group in the Illinois population which failed to become mature by the first fall, and which apparently survived into a second year. Therefore the survival of the majority of the yearling group in the Michigan population into the second year is a result which would be expected on the basis of the findings of the present study.

Large numbers of the yearling individuals in Creaser's population died during the fall or early winter of their second year. A similar though less marked mortality was noticed among members of the cor-

responding age group in the present study accompanying the onset of winter, and the greater mortality in the Michigan population may have been due to the more severe winter in the more northern latitude.

Furthermore, although Creaser does not mention the fact in his paper, the graphs representing his collections show indications of the presence of a few very large individuals corresponding to the occasional individuals of 35 to 40 mm. cephalothorax length which were found in the present study. This class is represented in Creaser's population by individuals measuring from 30 to 35 mm. cephalothorax length. This smaller size corresponds to the generally smaller size of the Michigan race of *C. propinquus* as compared to the Illinois race of the same species.

Thus the *C. propinquus* which Creaser studied, like those studied by the writer, probably die a natural death as yearlings, if they have reached sexual maturity by the first fall after they are hatched; and do not die a natural death until two years old if they have failed to reach sexual maturity by the first fall. Likewise occasional individuals among them probably live to be three years old. Apparently, therefore, Creaser's crayfish, like those studied by the writer, with few exceptions, if any, produce only a single brood of young during their lives.

Thus the question of the length of life of the individuals in this species seems to be quite definitely linked to the two factors of rapidity of growth and reproduction. Ortmann (1906) says: "Whether slow growth, including late development, influences total length of life cannot be ascertained." However, in view of the indications of the present study, supported by the evidence of the similar study made by Creaser in a different locality, having different climatic conditions, the conclusion seems inescapable that the two principal factors which determine length of life in this species are: (1) the rapidity of growth, influencing as it does the time of attainment of sexual maturity; and (2) the engaging in the reproductive activities themselves.

SUMMARY OF THE LIFE CYCLE

We may summarize the life cycle of *C. propinquus* as it occurs in east central Illinois as follows: The young are hatched in May or June, and remain attached to the mother for about one to two weeks, depending on the season. Following the second molt they become free-swimming and possess in general the form of the adult. At this time they measure about 5 mm. cephalothorax length.

They undergo a total of six to ten molts between the time of hatching and the end of the first growing season in late September or early October. By the end of the season they reach a size of 12 to 27 mm. cephalothorax length. The majority of them attain sexual maturity at this time, since the attainment of sexual maturity coincides

in general with the attainment of a size of approximately 20 mm. cephalothorax length.

Copulation occurs during the late fall and early spring and involves individuals of less than one year old if they are sufficiently large to be sexually mature. During the winter no molting takes place and the sizes of all individuals remain unchanged.

The eggs are laid in late March or early April, and are carried for a period of four to six weeks depending on the temperature. The females remain in seclusion during the period when the eggs are being laid, and also while the young are attached.

The adult males molt twice during the spring, changing from first form to second form with the first adult molt, and from second form back to first form with the second adult molt. The immature yearling group, both males and females, molt twice at the same times as the adult males, then a third time during May or June, and a fourth time in July or August. They attain sexual maturity as yearlings at the time of their second molt in the spring. The adult females molt only once. This molt occurs just after the young are shed in May or June.

No growth takes place among the adult yearling males or the immature group as a result of their first molt of spring, but a very marked growth in both groups accompanies the second spring molt. A similar growth accompanies the single adult female molt.

As a result of this growth the adult yearling males and females attain the ordinary maximum size of 25 to 35 mm. cephalothorax length. Immediately following the attainment of this size they die a natural death. This natural death involves all of the yearlings of both sexes which were adult during the winter and spring. Therefore it involves the majority of the yearling group.

The members of the yearling population which only attained maturity as yearlings survive during a second year. They attain the ordinary maximum size of 25 to 35 mm. cephalothorax length as a result of their third and fourth yearling molts. They produce a brood of young as two-year-olds, and most of them die at the beginning of their third year, along with the adult yearlings; but a very few, among which the females greatly outnumber the males, live over a third year. These individuals attain a size of 35 to 40 mm. cephalothorax length, which apparently constitutes an absolute maximum of size for the race.

The great majority of this species, therefore, die as yearlings. A small section of the population survives during a second year, and occasional individuals live to be three years old. All the available evidence indicates that most or all individuals of both sexes produce only a single brood of young.

CONCLUSIONS

ENVIRONMENTAL RELATIONS

1. The young *C. propinquus* live in the surface water of the stream during most of their first summer.
2. The adults are bottom-dwellers at all seasons.
3. Members of all size groups seek the deeper portions of the stream during the winter.
4. Individuals of this species are positive to sunlight at all seasons.

LIFE CYCLE

1. The young are hatched in May or June and remain attached to the mother about one to two weeks, during which time they probably undergo two molts.
2. At the time they become free-swimming they measure about 5 mm. cephalothorax length.
3. They undergo a total of 6 to 10 molts during the first growing season, and attain a cephalothorax length of 12 to 27 mm.
4. Sexual maturity in both sexes is attained coincident with a cephalothorax length of about 20 mm.
5. The majority of the season's young normally attain sexual maturity by the first fall after they are hatched at the latitude of Urbana, Illinois.
6. During the winter no growth or molting takes place and the sizes of all individuals remain unchanged.
7. Copulation occurs during the late fall and early spring at the latitude of Urbana, Illinois.
8. The eggs are laid in late March or early April, and are carried for a period of 4 to 6 weeks, depending on the temperature.
9. The adult males molt twice during the spring or early summer, changing to second form with the first adult molt, and reverting to first form with the second adult molt.
10. The immature yearling group of both sexes apparently molt four times during their second year. They attain sexual maturity with the second yearling molt.
11. The adult females undergo a single molt immediately following the shedding of the young in the spring.
12. Apparently no growth takes place in connection with the first yearling molt, among either mature males or immature individuals; but marked growth occurs in connection with the second yearling molt in both groups.
13. A similar growth takes place as a result of the single molt among the adult yearling females.

14. The portion of the young of the previous year which reached sexual maturity by the end of their first growing season, produce a brood of young the following spring, attain maximum size as a result of the second adult molt of the males and the single adult molt of the females, and die as yearlings.

15. The group which failed to attain maturity by the end of their first growing season live over a second year; attain maximum size during their second summer, produce a brood of young in their second spring, and for the most part die as two-year-olds.

16. A very few individuals, among which females predominate, survive over a third year, and produce a brood of young in their third spring.

17. With the possible exception of the few which live to be three years old, the individuals of this species apparently produce only a single brood of young during their lives.

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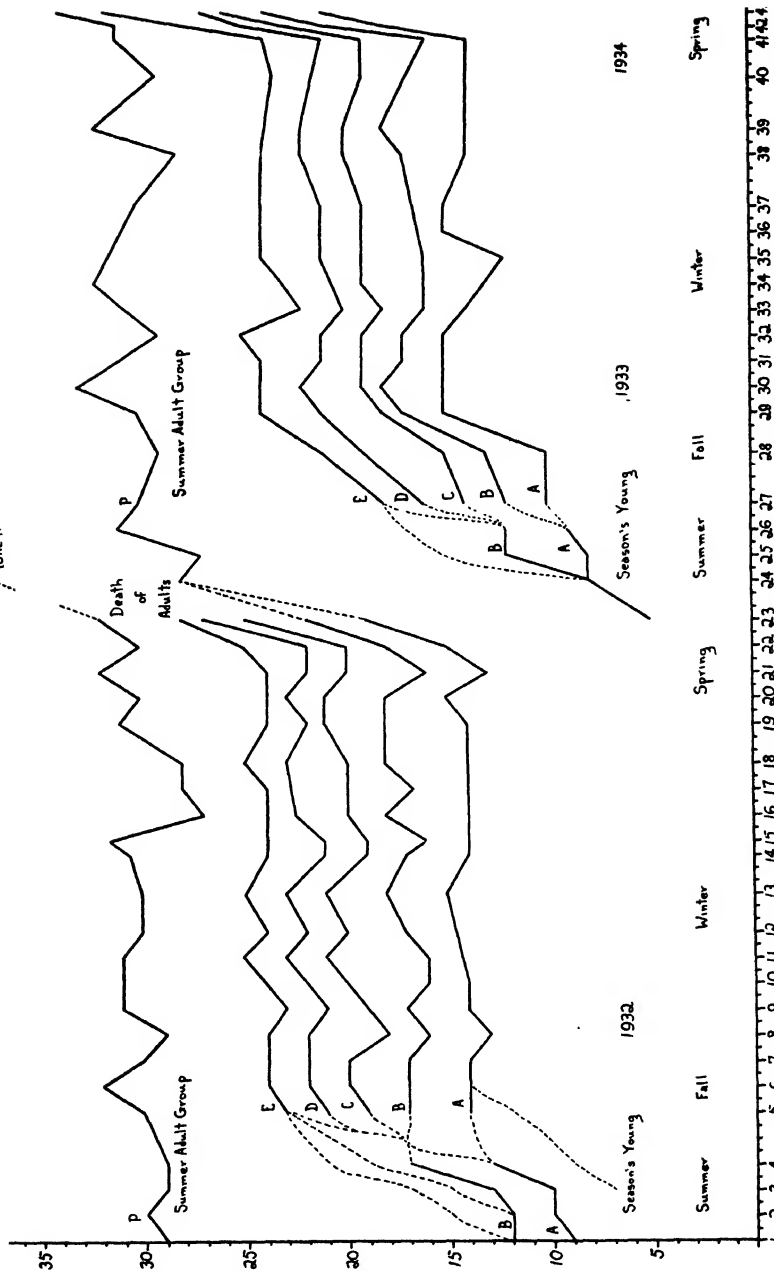
GRAPHS

The collections taken during the two years in which this study was in progress are represented by the following series of forty-four graphs. Of these, forty-three (Graphs 4 to 46, inclusive) represent individual collections, arranged chronologically. On these graphs the abscissa represents cephalothorax length in millimeters, and the ordinate represents number of individuals; the total population is indicated by a solid line, the females by a broken line, and the males by a dotted line.

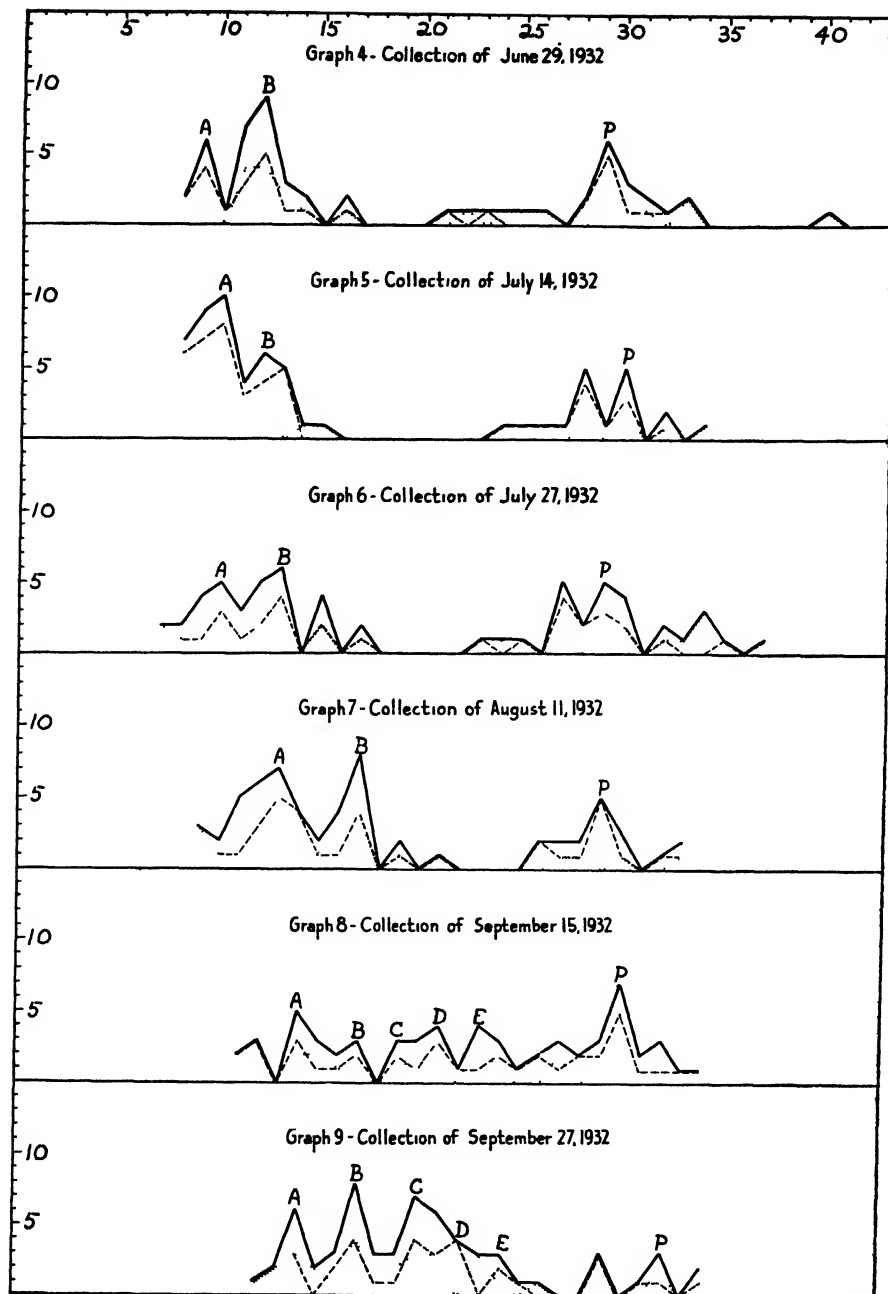
The first graph of the series (Graph 3) is the composite graph, showing the progress of the modes, representing the size groups. The abscissa represents time in weeks, while the ordinate represents the position of the modes in millimeters. The letters A, B, C, D, E, and P on the lines of this graph refer to the corresponding letters on the modes of the graphs of individual collections. Each line on the composite graph thus represents the development and history of a particular size group in the population. Each number on the abscissa represents a single collection. In the following list the dates of the collections are given with the corresponding numbers shown in Graph 3:

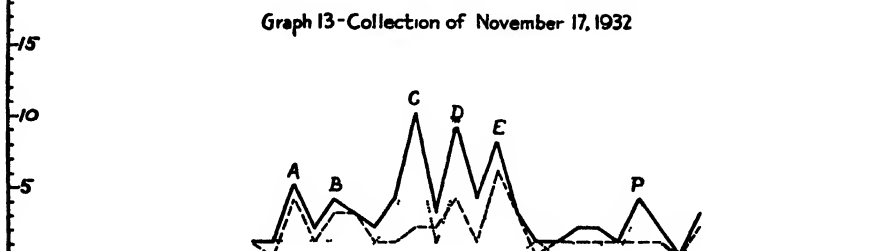
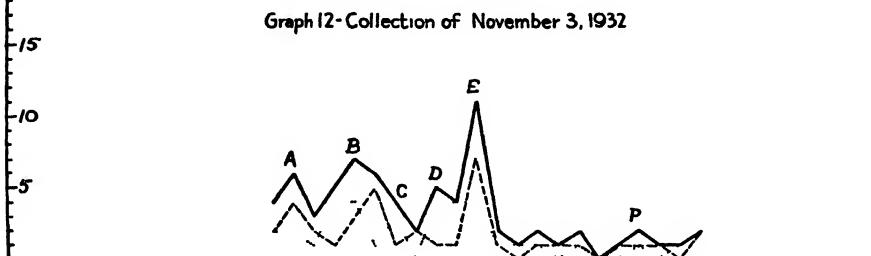
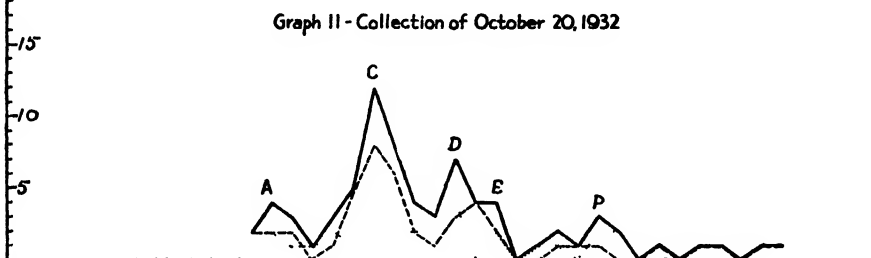
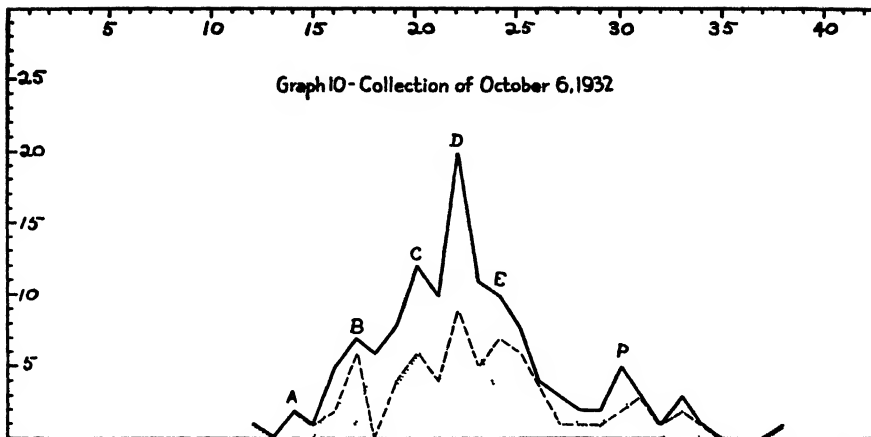
- | | |
|-----------------------|------------------------|
| 1. June 29, 1932 | 23. June 7, 1933 |
| 2. July 14, 1932 | 24. June 25, 1933 |
| 3. July 27, 1932 | 25. July 10, 1933 |
| 4. August 11, 1932 | 26. July 22, 1933 |
| 5. September 15, 1932 | 27. August 5, 1933 |
| 6. September 27, 1932 | 28. August 31, 1933 |
| 7. October 6, 1932 | 29. September 20, 1933 |
| 8. October 20, 1932 | 30. October 7, 1933 |
| 9. November 3, 1932 | 31. October 24, 1933 |
| 10. November 17, 1932 | 32. November 4, 1933 |
| 11. December 1, 1932 | 33. November 18, 1933 |
| 12. December 17, 1932 | 34. December 6, 1933 |
| 13. January 5, 1933 | 35. December 20, 1933 |
| 14. January 26, 1933 | 36. January 6, 1934 |
| 15. February 2, 1933 | 37. January 20, 1934 |
| 16. February 18, 1933 | 38. February 17, 1934 |
| 17. March 4, 1933 | 39. March 4, 1934 |
| 18. March 18, 1933 | 40. April 7, 1934 |
| 19. April 8, 1933 | 41. April 28, 1934 |
| 20. April 22, 1933 | 42. May 5, 1934 |
| 21. May 6, 1933 | 43. May 13, 1934 |
| 22. May 21, 1933 | |

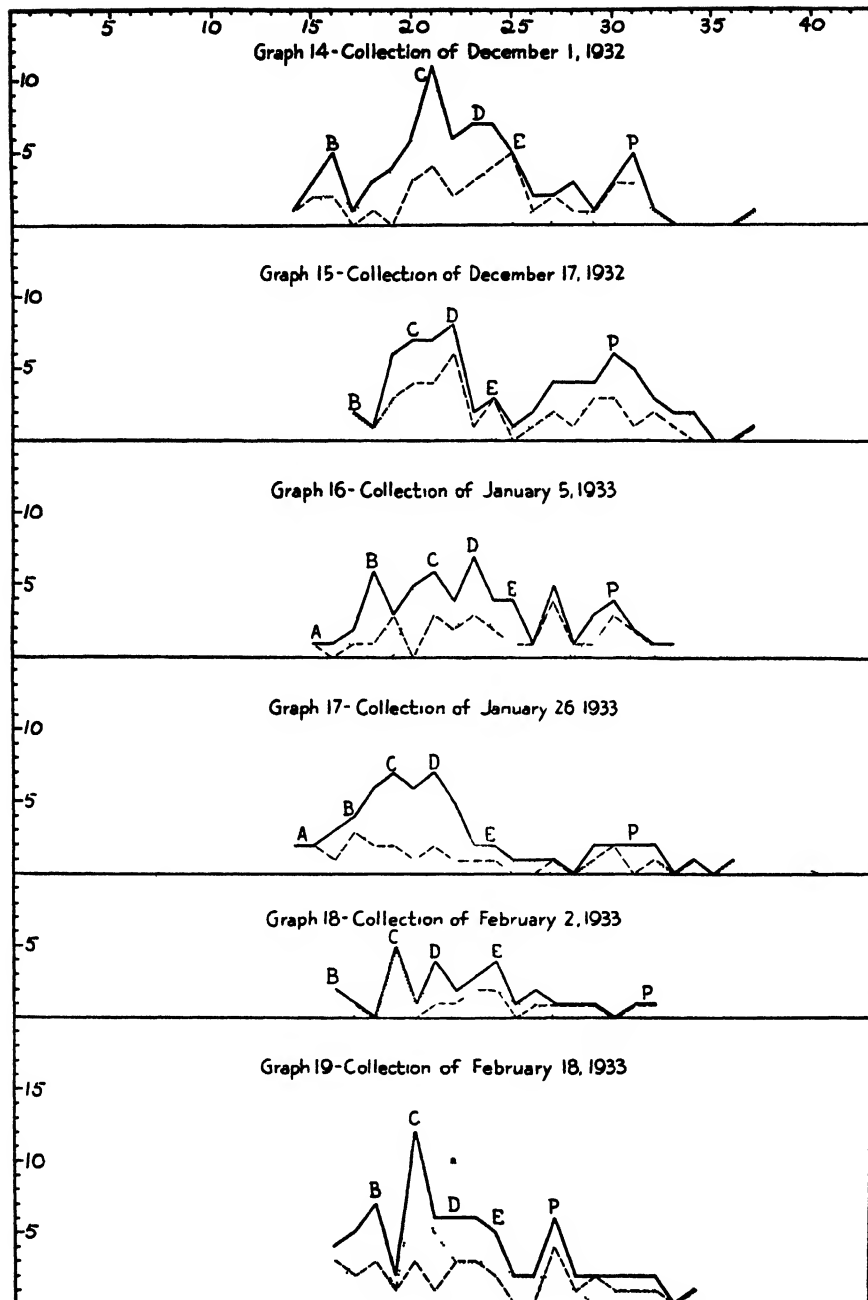
Graph 3-Composite Graph
(One 1.)

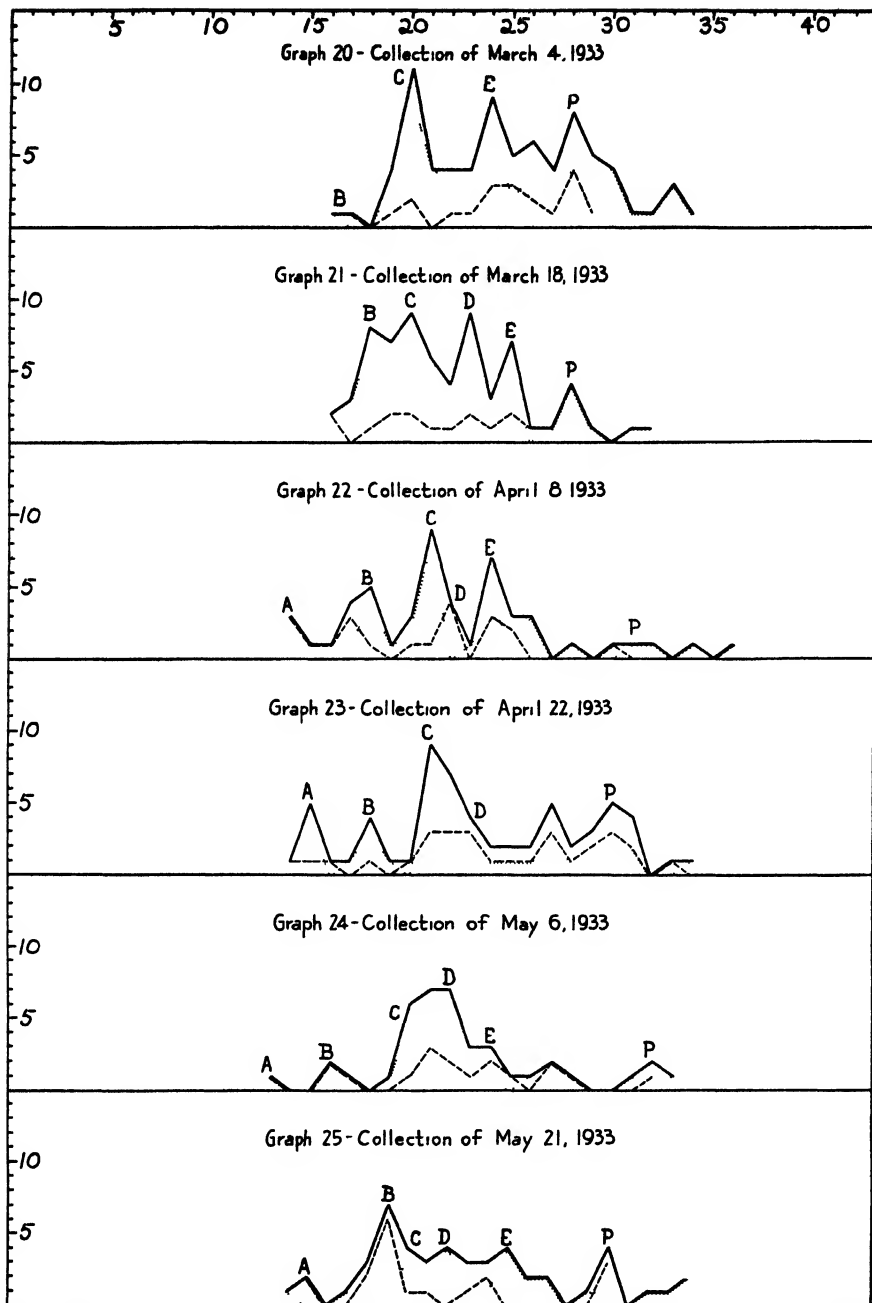


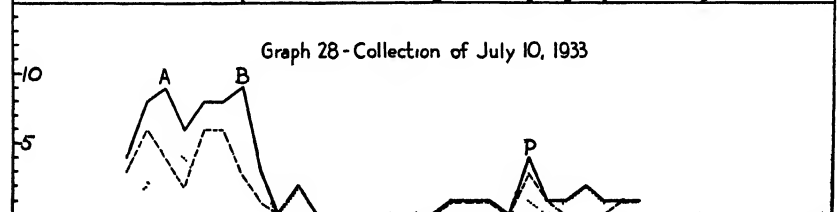
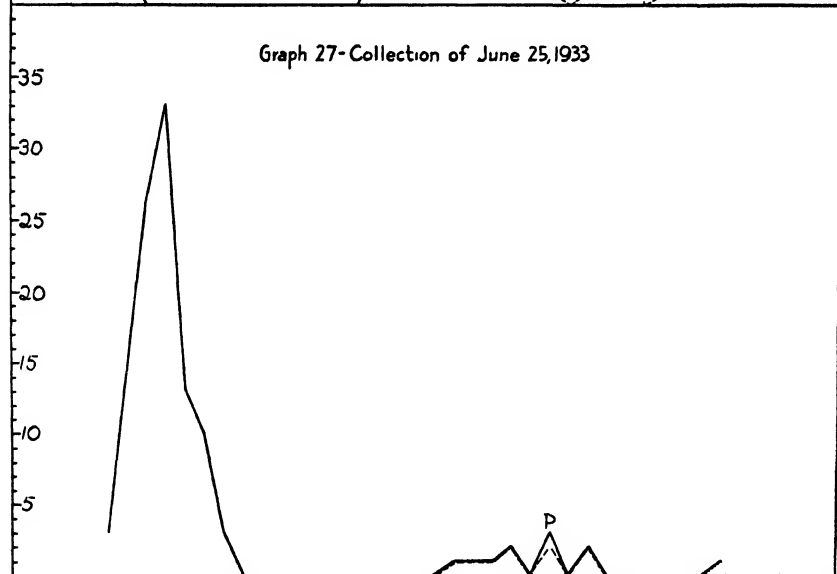
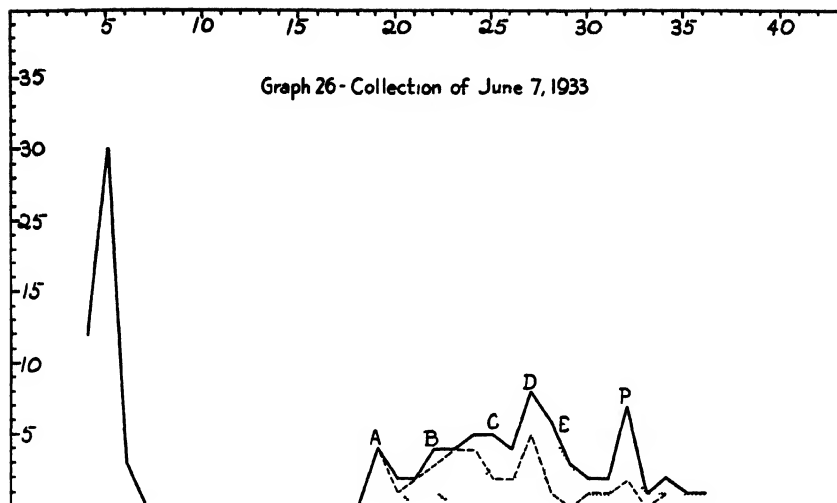
For explanation see page 57.

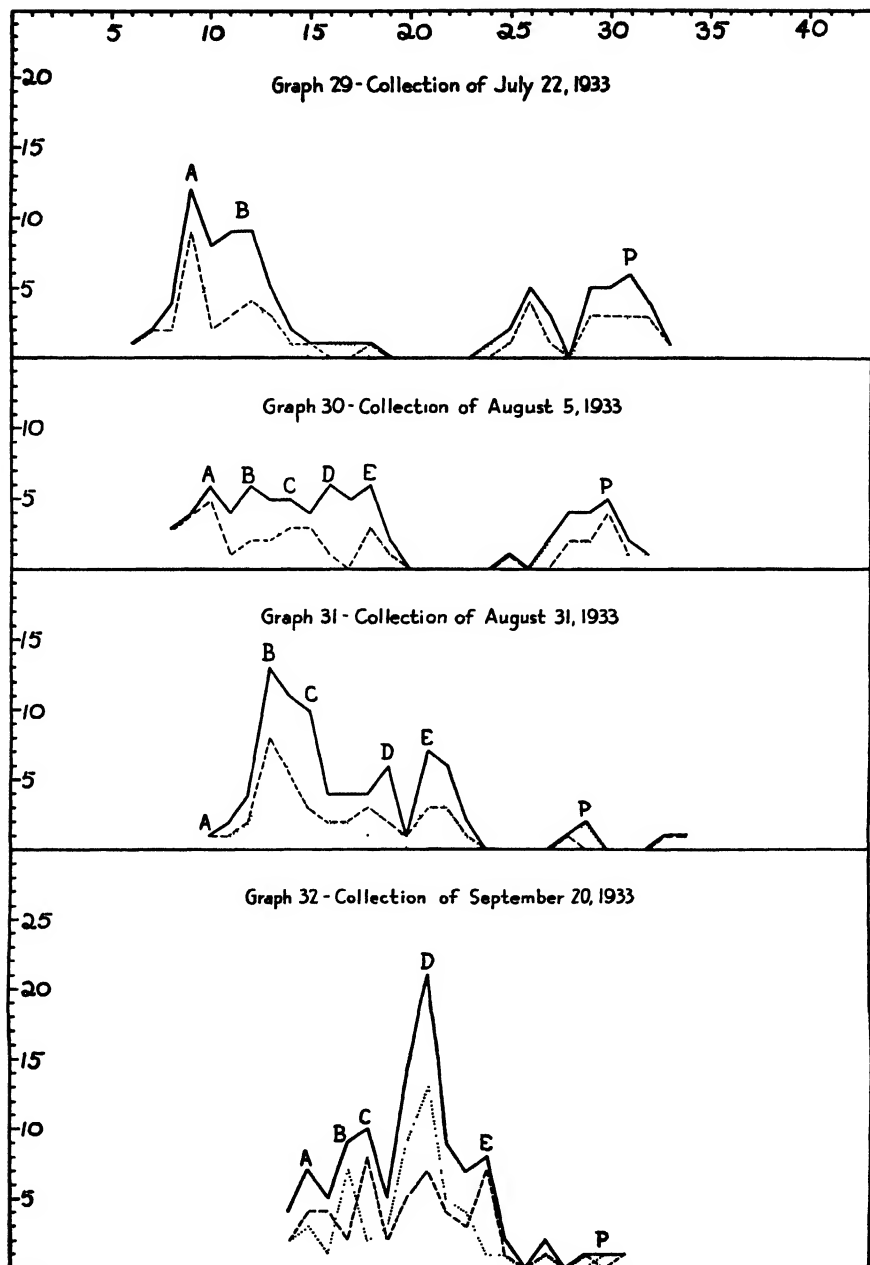


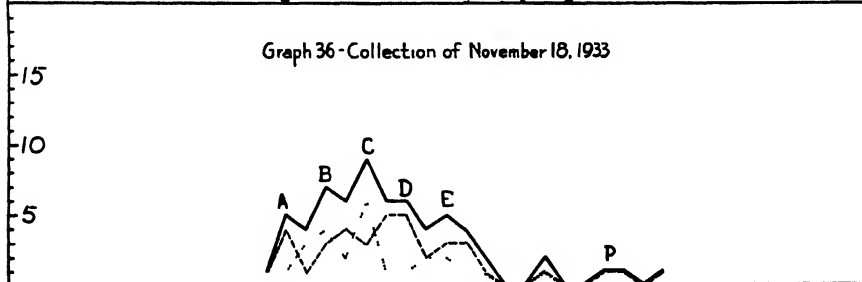
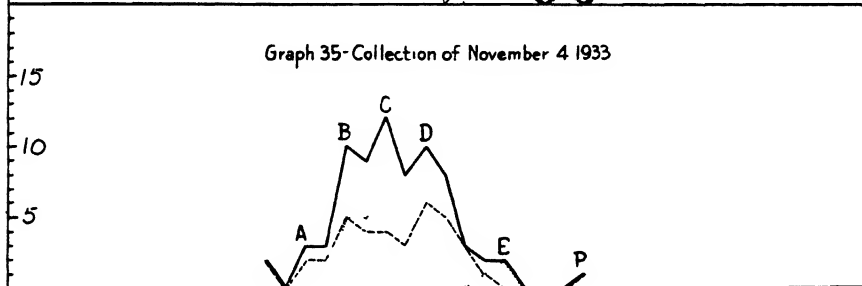
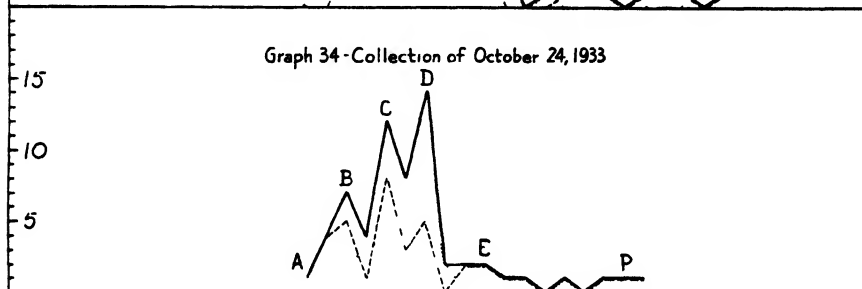
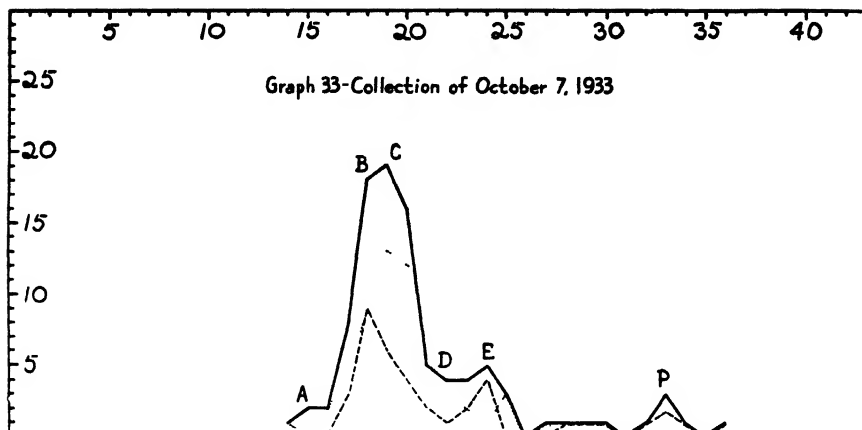


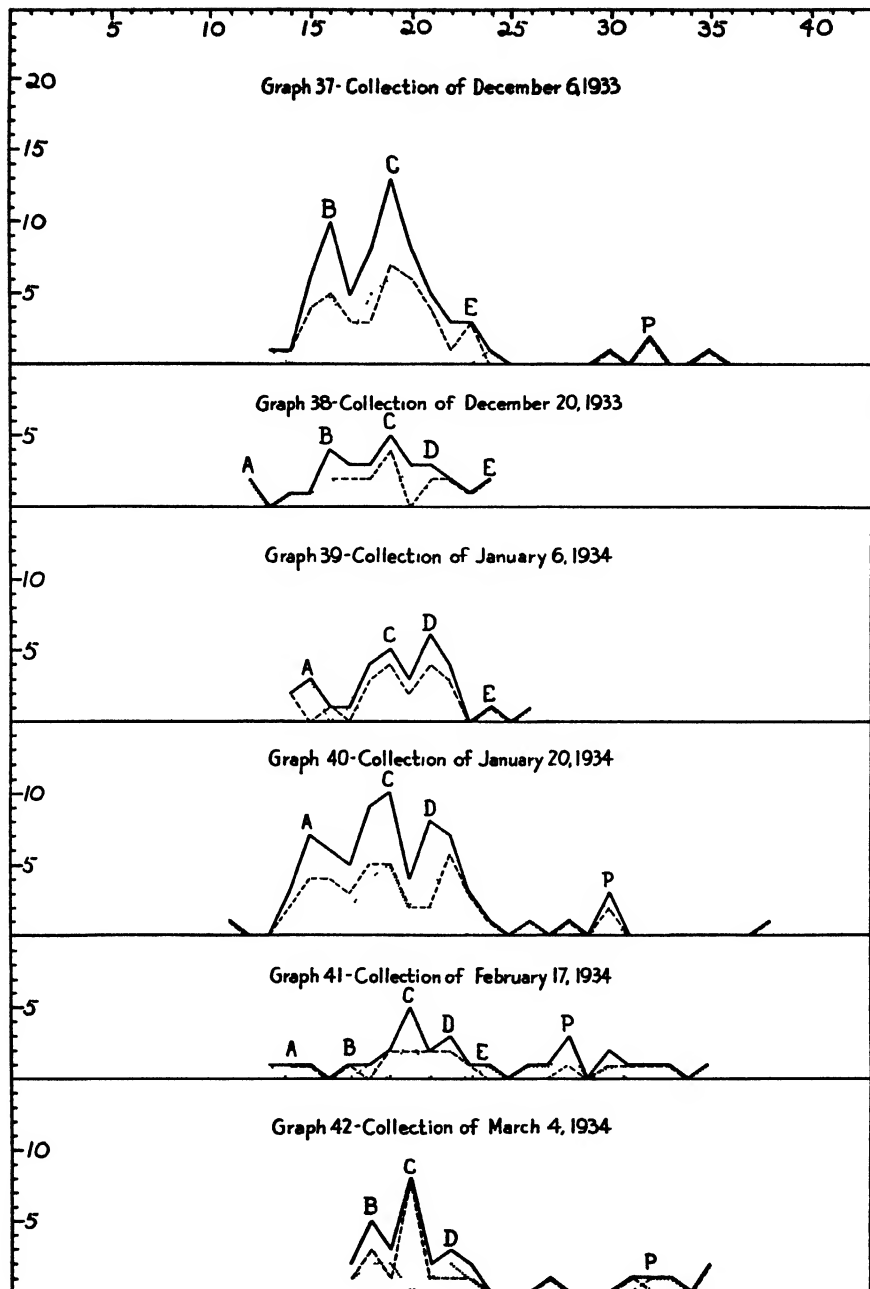


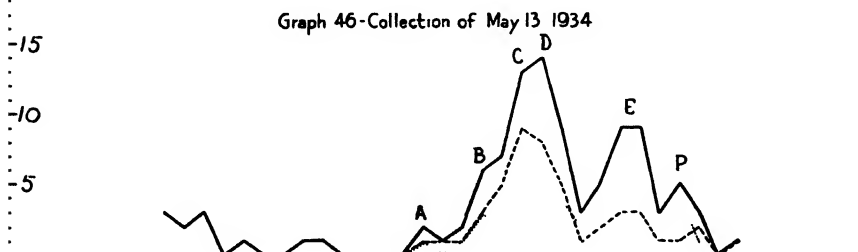
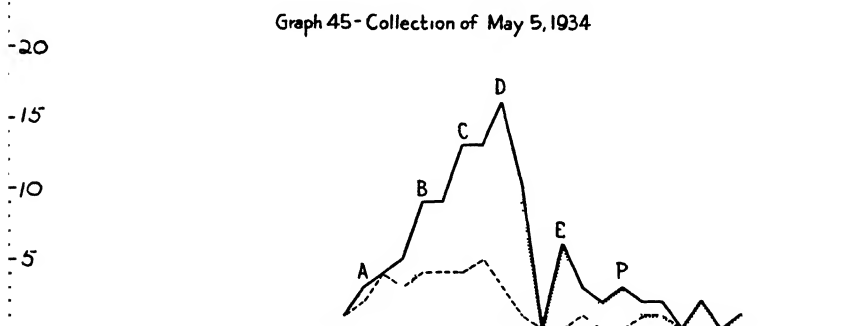
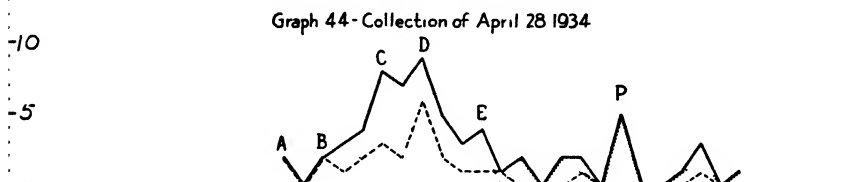
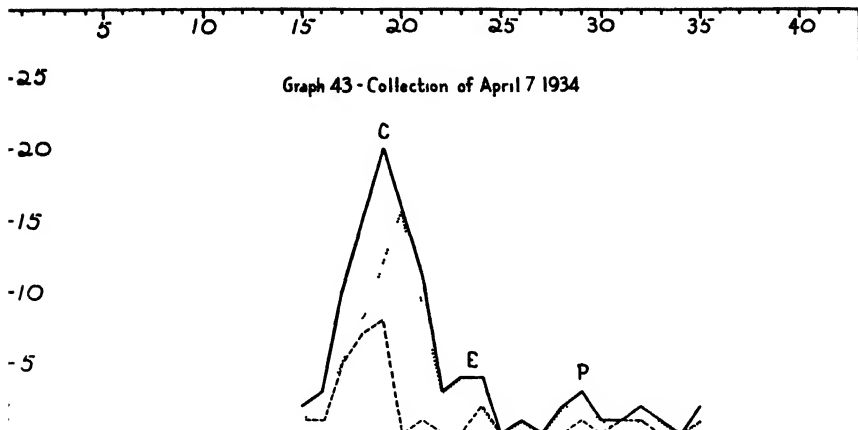












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TAXONOMIC STUDIES ON THE MOUTH PARTS OF LARVAL ANURA

WITH THREE FIGURES AND EIGHT CHARTS

BY
RAY JANNEY NICHOLS

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
UNIVERSITY OF ILLINOIS
No. 510

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INTRODUCTION

After some years of using Wright's "Synopsis and Description of North American Tadpoles" (1929), and after discussing various aspects of the paper upon several occasions with Dr. H. J. Van Cleave, it was decided that certain aspects merited further investigation. These were, namely, (1) the uncertain specificity of some described tadpoles, (2) the acknowledged application of the characters used in classifying tadpoles to only "mature" tadpoles, (3) the use of certain relative measurements as taxonomic characters, particularly those of the rows of horny teeth and the beaks of the larval mouth apparatus, without any statement as to the reliability of such relative measurements or as to how and why the particular relative measurements used were chosen. It was at once obviously desirable (1) to determine the applicability to younger tadpoles of characters used in distinguishing "mature" tadpoles, and (2) to determine whether or not there exists any sound and reliable basis for using relative measurements.

It was decided to use the temporary larval mouth apparatus as the object of this study. There were several reasons for choosing the mouth apparatus as an object for such a study. Should it afford satisfactorily constant taxonomic characters, they would be preferable to other characters, because the mouth apparatus will withstand the "hardships of preservation" with less alteration of character than will perhaps any other structure or feature of the tadpole. The body or tail may become torn or shriveled, and colors may fade; but the mouth apparatus remains relatively intact. Also, although taking measurements of small rows of teeth may become tedious, such measurements can be obtained with a great deal more accuracy than is forthcoming from an attempt to determine whether certain spots are "pinkish cinnamon" or "apricot buff"!

The larval mouth apparatus (Fig. 1) is composed of two lips, an upper and a lower. These so-called lips are not entirely separate or distinct; and the apparatus thus has the general shape and appearance of a somewhat flattened or slightly concave disc when the lips are not rolled or curled at the edges. For this reason the apparatus is frequently spoken of as a funnel or disc, and will hereinafter be designated as the "oral disc." The laterally-extending diameter of this disc may be somewhat greater than the antero-posterior diameter. The disc is bordered to a varying extent with papillae, the exact extent and number of rows of which vary in different families and genera. In the center of the disc is the mouth opening, which is immediately bounded by upper and lower

"horny" mandibles or beaks. The term "beak," or "horny beak," is more nearly appropriate and avoids confusion. Accordingly, these "horny" beaks will hereinafter be referred to as "upper beak" and "lower beak" respectively. Situated more or less concentrically on the disc are ridges, each of which bears one or two rows of teeth, which teeth are keratinized cells. The number and disposition of these rows of teeth vary in different groups.

However, the number and approximate disposition of the rows of teeth are similar in the species included in this study. A description of the features in common follows.

There is only one row of teeth on a ridge. The rows have the following distribution (Fig. 1): There is an extreme anterior or upper row extending almost completely across the disc. This row is designated variously by different authors (cf. below under "Historical Review"). The more pertinent term, especially when comparing it with other rows of teeth, seems to be "first upper labial row." A second row of teeth is located posterior and/or ventral to the first upper labial row. The lateral ends of this second row are approximately even with those of the first

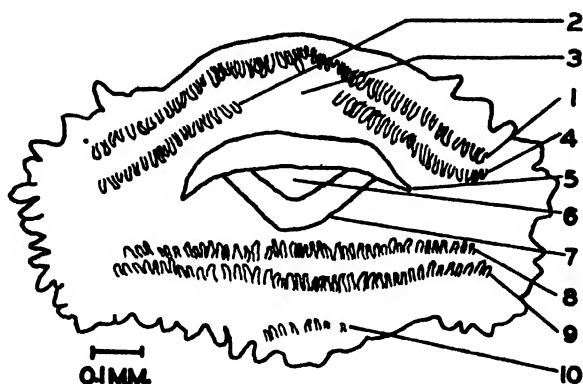


FIG. 1.—Camera lucida drawing of mouth parts of a tadpole of *Pseudacris nigrita triseriata* to show arrangement of teeth. (Body length of specimen, 3.57 mm.)

Key

- | | |
|----------------------------------------------|------------------------------|
| 1. First upper row of teeth | 5. Upper beak |
| 2. Right part of second upper row of teeth | 6. Mouth opening |
| 3. Median space in second upper row of teeth | 7. Lower beak |
| 4. Left part of second upper row of teeth | 8. First lower row of teeth |
| | 9. Second lower row of teeth |
| | 10. Third lower row of teeth |

upper row. However, there is a median space devoid of teeth that interrupts the second row, dividing it into right and left parts. This second row is the "second upper labial row."

Below and/or posterior to the mouth opening are three rows of teeth, each of which is more or less complete. There are exceptions which will be discussed later under the heading of the species concerned. These rows are respectively from nearest the mouth opening toward the periphery of the disc "first lower labial row," "second lower labial row," and "third lower labial row." The first and second of these lower rows are approximately of equal lengths and are slightly shorter than the upper rows. The third of the lower rows is shorter than any other row.

Since all the rows are "labial" rows, the terminology adopted for use throughout this study has been shortened and may be introduced at this point as follows (cf. labels of Fig. 1): The first upper labial row is designated as the "first upper row." The second upper labial row is designated as the "second upper row" when the row is referred to as a unit or a *single* row. When reference is to the right or left parts of this row, the terms, "right part of the second upper row," or "left part of the second upper row," are used respectively. The toothless space between the right and left parts is designated as the "median space in the second upper row." The lower rows of teeth are designated respectively as "first lower row," "second lower row," and "third lower row." The first and second upper and first and second lower rows are frequently referred to as the "four longer rows."

The taxonomic characters involving the rows of teeth and the horny beaks that have been used are (1) numbers of rows of teeth, (2) the location of these rows, and (3) the ratios between the lengths of certain rows of teeth and between the length of a given row of teeth and the lateral length of the upper beak. It was decided ultimately to restrict this study to these ratios, or relative measurements, with particular respect to their constancy or variation in tadpoles of different sizes or ages.

In order to study the mouth apparatus in tadpoles of different ages, it was first necessary to secure series of tadpoles of as nearly uniform hereditary constitution as possible and reared under identical conditions so that identity could not be questionable, and so that variation that might occur in individuals of a series could only be attributed to the normal tendency of a given hereditary complex to vary. Collections were made in Mississippi in 1932 and in Illinois and Indiana in 1933.

A review of the literature revealed only the use of relative measurements of the rows of teeth—that is, the relation of the length of one row of teeth to the length of another row of teeth—in identifying mature tadpoles without revealing any systematic study of the constancy of these

relative measurements at different ages, or of the basis, real or imaginary, of using such relative measurements at all.

The next step in the study was the taking of various measurements of the body and mouthparts, i.e., rows of teeth and the horny beaks, of each tadpole of each of the series collected. Then a study was made of relative measurements, which were obtained graphically from the actual measurements by plotting various combinations of the latter. From these analyses and studies certain conclusions have been drawn, namely, as to a method and an explainable basis for the use of relative measurements of the mouthparts, as to the combinations of actual measurements affording the most constant relative measurements at all ages, and as to the specific distinctiveness of these relative measurements, and finally as to the reliability of the use of such relative measurements as taxonomic characters.

HISTORICAL REVIEW

A careful survey of the literature has failed to disclose any previous attempts at an analysis such as is made in the present study of the growth phenomena of the parts of the mouth apparatus of tadpoles. Neither has anyone attempted to determine the constancy or lack of constancy at different ages of such ratios of measurements of mouthparts as are used as taxonomic characters. The general attitude seems to have been to limit such characterizations to fully grown tadpoles, with either no indication of the degree of applicability to younger tadpoles of such characterizations, or with an acknowledgment of the limited use to which the characters may be put taxonomically. However, studies on the mouthparts of larval Anura have been abundant, and various characters afforded by the mouthparts have been recognized and recorded by many authors. Therefore, to afford a historical background for the present study, the course of the development of the particularly taxonomic studies on the mouthparts of larval Anura will be reviewed. Reference will also be made to outstanding studies of other than taxonomic aspects.

The earliest reference to studies of any kind on the mouthparts of larval Anura seems to be that made to the *Biblia Naturae* of Swammerdam published in 1738. Swammerdam described and figured the mouth apparatus of a tadpole, distinguishing and describing the individual parts. However, it was approximately a century later before any other observations on mouthparts were made. The first published descriptions after this lapse of a century were those by Martin Saint-Ange in 1831 and Duges in 1834. The first recorded investigation into the formation and development of the horny teeth and mandibles was that of Carl Vogt, published in 1842. He made histological studies of the formation and structure of the teeth and of the mandibles.

Stricker in 1857 described the structure of the papillae of the oral disc and attributed to them the function of tactile organs. Meanwhile various observers had published less pioneer articles involving only mere mention or general descriptions, or treating the histogenesis of the teeth.

The publication marking the beginning of the use of features of the mouth apparatus as taxonomic characters was a paper by Van Bambeke appearing in 1863. He studied the formation and structure of the teeth, mandibles, and papillae of four European species and called especial attention to the fact that there were distinct differences between the respective parts of the mouth apparatus in the different species studied by him. This is the first recorded instance in which attention is called to the fact that differences in the mouth apparatus of different species do exist.

Leydig, in 1874, also called attention to the differences in form and disposition of the mouthparts in different species. Lataste, in 1879, accorded taxonomic value to the forms of individual teeth in different species.

The first detailed studies on differences in the parts of the mouth apparatus in several different species appeared almost simultaneously in America and in Europe. The European publication was a "preliminary communication" by Heron-Royer and Van Bambeke, in which the mouth apparatus of tadpoles of six European species of Anura were described. This "preliminary communication" was followed by a series of papers by Heron-Royer, in which papers the mouth apparatus of more species was described. A final paper by both authors, i.e., Heron-Royer and Van Bambeke appeared in 1889. In this paper are treated the formations of the teeth and mandibles and papillae; but more important from the point of view of the present study are the descriptions of the mouth apparatus in tadpoles of twenty-two species of European toads and frogs. In addition, the distinguishing characters of different species, the characters in common possessed by species of a given genus, and characters possessed by all genera of a family are pointed out. The characters used as taxonomic by these authors are the shape of the oral disc, the number of rows of teeth on a ridge, the number and disposition of the rows of teeth, any peculiarities of the mandibles, and the characters of the individual teeth. However, relative measurements of rows of teeth were not used.

Meanwhile, in January 1882, Mary Hinckley communicated to the Boston Society of Natural History a paper "On some differences in mouth structure of tadpoles of Anourous Batrachians found in Milton, Mass." Miss Hinckley's paper was published only a few months (nine) after the preliminary communication of Heron-Royer and Van Bambeke. That Miss Hinckley was unaware of this European publication when writing her paper is indicated by the fact that she acknowledges the same

in a "note" at the end of her paper. Therefore, the two papers may be considered as concurrent. And it is of interest and of note that two such similar studies were under way coincidentally in old and new worlds. Miss Hinckley's paper marked the advent of Americans into the development of the study at hand.

She described the mouth apparatus of tadpoles of nine species, pointing out the family, generic, and specific differences. The characters she used are form of oral disc ("lips"), number, color, and distribution of papillae, and number and disposition of rows of teeth ("fringed folds"). She states, "After the parts of the mouth are developed I have observed no change of form in the folds or papillae." The meaning of this statement depends altogether on how "change of form . . ." is to be interpreted. Presumably, the intended meaning is that the general pattern of the oral disc (or "lips") and its parts remains about the same. If Miss Hinckley meant that the outlines, proportionate lengths, and interruptions of the rows of teeth ("fringed folds") remain unchanged, her statement must be challenged on the basis of the results of the present study.

She also pointed out that in the Ranidae the papillae are quite frequently replaced by or bear short groups of teeth.

Other papers appearing before the final work of Heron-Royer and Van Bambeke are those by Schultze and by Keiffer in 1888. Both authors treated the formation and distribution of the horny teeth in their respective studies. In 1890 Gutzeit published an account of his studies, both gross and histological, on the formation of the horny teeth and mandibles.

In 1891 G. A. Boulenger published "A Synopsis of the Tadpoles of the European Batrachians." The synopsis is of all larval characters, with considerable attention paid to those of the mouth apparatus. In addition to the characters of the mouth apparatus used by previous authors, Boulenger introduced the use as taxonomic characters of the relationships between the lengths of different rows of teeth. The only rows he used for such purposes were the second and third lower rows, expressing the third lower row as being a certain fraction of the second lower row. It might be stated at this point that Boulenger numbered the lower rows of teeth from the periphery toward the mandible, this method of numbering the lower rows of teeth being the reverse of that used in the present study. The reference above to second and third lower rows is according to the method of numbering used in the present study. Boulenger also described the second upper row ("series") as being "widely" or "narrowly" interrupted. This could, however, hardly be termed a very exact description of the relative width of the median space in the second upper row. As mentioned above, the relation of the length

of the third lower row of teeth to the length of the second lower row was expressed as a definite fraction. Therefore, this publication by Boulenger must be considered as marking the beginning of the use of such exact relative measurements of rows of teeth as taxonomic characters. Attention may also be called to the fact that the character descriptions in Boulenger's paper refer only to fully grown tadpoles. To quote his statement, "The development of the larvae is left out of consideration; my descriptions apply merely to the fully-developed tadpole, in the condition generally known as the "third period" in the larval development, the period between the budding of the hind limbs and the bursting out of the fore limbs."

Practically the same synopsis is included in the section on tadpoles of Boulenger's *The Tailless Batrachia of Europe* (1897).

Since these early works no attempts at comprehensive synopses of larval Anura have been made until within recent years. However, many descriptions of tadpoles examined have included a description of the mouth apparatus as a part of the routine description. The characters of the mouth apparatus described are invariably the shape of the oral disc, and the number and distribution of the rows of teeth. Yet, no use seems to have been made generally of the relationships existing between the lengths of rows of teeth as taxonomic characters.

From the time of Miss Hinckley's rather brief paper in 1882 no one attempted a comprehensive survey of the American tadpoles until 1929, when Wright's "Synopsis and description of North American tadpoles" appeared. This was preceded by Wright's "Life Histories of the Anura of Ithaca, New York," which appeared in 1914. These rather widely separated publications represent, according to their author's introductions; studies which began in 1906-1907. Relative measurements of the rows of teeth and the upper mandible were used in characterizing the tadpoles of the eight different species treated in the earlier publication (Wright, 1914). However, since the same species are treated and the same relative measurements are used in the later publication (Wright, 1929), detailed review will be restricted to the latter.

Although this synopsis (Wright, 1929: p. 2.) is specified as applying only to "mature" larvae, since "Half-grown larvae . . . are often quite abnormal in the usual characters used in larval descriptions" yet rather abundant utilization is made of relative measurements of and ratios between different rows of teeth and/or certain rows of teeth and the upper beak as taxonomic characters. Therefore, this latter being true, and, since the synopsis forms the "point of departure" for the present study, those parts of the synopsis dealing with characters of the horny teeth and beaks may be noted more fully.

If the synopsis or key (Wright, 1929) be examined for the different relative measurements of rows of teeth and/or of rows of teeth and upper beak; and, if the interpretations of many questionable statements be the same as made here, not less than fifty different expressions will be encountered, each being used from one to twenty times. Of these fifty or more ways of expressing the relative measurements used, not less than fifteen are either mathematical impossibilities or of very uncertain meaning.

Further, the number of different terms applied to what is presumably the chord length of a given row or of the upper beak is apparently infinite, and the order of description of various characters is not at all uniform. In a continuous discussion, variations of a given term might be justified as avoiding monotonous repetition without being confusing. But such variations in terms in isolated phrases of a synopsis are both unnecessary and confusing.

It is, of course, obvious that many expressions of relative lengths are synonymous; but more are synonymous than are at first apparent. It might be surprising to discover that relationships of only nine different combinations of lengths of rows and of rows and upper beak are expressed. These nine relationships of lengths or relative lengths could be expressed as simple ratios (of chord lengths), the ratios being expressed as ratios to one. The nine combinations actually involved in the synopsis are as follows: (1) first upper row/second upper row; (2) first lower row/third lower row; (3) second lower row/third lower row; (4) median space in second upper row/right or left parts of the second upper row; (5) first upper row/upper beak; (6) second upper row/upper beak; (7) first lower row/upper beak; (8) second lower row/upper beak; (9) third lower row/upper beak.

Aside from rather questionable or ambiguous statements and lack of uniformity in terminology, attention may be directed to the irregular sequence in the listing of characters in the synopsis. It could be that the order in which characters are listed is an order of importance in being distinctive, although no statement to this effect has been found.

The foregoing has been no attempt to belittle the synopsis (Wright 1929). Rather, it is to be regretted, after such an expenditure of time and effort in collecting the tremendous amount of data which form the basis of the synopsis, that such lack of uniformity in arrangement, presentation, and expression of the material at hand should detract from the usefulness and value of the synopsis.

Since the present study was begun, *Frogs of the Okefinokee* (Wright 1932) and *Handbook of Frogs and Toads* (Wright and Wright 1933) have been published. In the latter publication relative measurements of

the rows of teeth are not used in characterizing tadpoles of the different species of frogs and toads. In the former publication (Wright 1932) the synopsis from the 1929 publication is used verbatim except for the omission of the descriptions of twelve species not occurring in the Okefinokee swamp. Eight species not occurring in the Okefinokee swamp are retained in the synopsis, of which eight species three "should" occur in the swamp. However, two other species that do occur and three others that "should" occur in the Okefinokee swamp are not included in the 1932 version of the synopsis. The "*Bufo (Raleigh)*" of the 1929 synopsis is changed to "*Bufo fowleri*" in the 1932 version. Otherwise the two synopses are identical and the later one need be discussed no further.

Noble (1931) does not think that characters of the mouth apparatus have any value as indicating relationships, but does infer that they may afford taxonomic characters. In discussing the value of larval characters in classification, Noble (1926) makes no reference to such characters as form the basis of this study.

The only publication to date that has dealt specifically with variations in the mouth apparatus of tadpoles is a study by Scott-Biraben and Fernandez-Marcinowski that appeared in 1921. Their studies were on groups of tadpoles and treated only variations in number and disposition of the rows of teeth, rows irregularly placed, the substitution of groups of teeth for papillae, the extension of rows of teeth by the appearance of teeth through the papillary border of the oral disc, etc. It may be recalled that Hinckley (1882) also called attention to certain of these variations. However, in no instance have such studies been carried out on a series of tadpoles graded consecutively with respect to age or size.

Considerable reference has been made during the course of this study to Huxley's *Problems of Relative Growth* (1932).

The historical background for this study on the mouth apparatus of tadpoles may be summarized as follows: The mouth apparatus was first described and figured by Swammerdam in 1738, first studied histologically (as to formation of parts) by Vogt in 1842, first recognized as affording taxonomic characters by Van Bambeke in 1863, first studied extensively for specific characters by Heron-Royer and Van Bambeke in Europe in 1881-1889 and by Hinckley in America in 1882, first used as affording specific relative measurements by G. A. Boulenger in a synopsis of European tadpoles in 1891, first studied extensively in American tadpoles for specific relative measurements by Wright in 1914-1929, and first studied particularly as to variations in parts by Scott-Biraben and Fernandez-Marcinowski in 1921, but has never been studied as to constancy (or variation) of specific relative measurements at different (particularly young and intermediate) ages until the present.

MATERIALS AND METHODS

COLLECTIONS

Pseudacris nigrita triseriata.—The series of tadpoles of *Pseudacris nigrita triseriata* used in this study were reared from the eggs obtained from field-mated pairs taken between 8:00 and 10:00 P.M., March 31, 1932, from a temporary swamp west of Clinton, Mississippi. Each pair taken in amplexus was placed immediately in a separate container. At about 10:30 P.M. these pairs were transferred to separate battery jars. The battery jars contained about two and one-half or three inches of water, in which had been placed a few twigs and dead grass stems. Each battery jar was covered with gauze held in place by rubber bands. All pairs had produced eggs by seven o'clock the next morning. These clutches of eggs were removed to separate containers and allowed to develop. Elodea and algae were kept in the battery jars in which the tadpoles developed.

Samples of from two to six specimens were taken twice daily from April 3rd to April 20th, and once daily thereafter until the supply of tadpoles was exhausted (May 1st). The tadpoles were fixed in Bouin's fluid, and, after the routine washing in alcohols, were finally preserved in 75-80% alcohol. Samples from different clutches of eggs were of course kept separate. However, the studies here reported have shown complete intermingling of characters, so that absolutely no distinction on any basis could be made between the individuals from different parents. All the mated pairs were preserved in formalin on April 4th. Identification of these pairs has recently been made by Dr. G. K. Noble, of the American Museum of Natural History, New York City.

Bufo fowleri.—Eggs were taken in the late afternoon of April 20, 1933, from a small puddle of water in the lily pond on the south campus of the University of Illinois. These eggs are known to have been deposited during the same afternoon in which they were collected. Only *B. fowleri* were observed at this time or at any time during the several days of excessive spawning activity.

The tadpoles were reared in battery jars in which were kept algae and Elodea. The diet of the tadpoles was supplemented with "Justrite" fish food and with fresh beef and liver. The water in the battery jars was kept fresh; and approximately the same number of tadpoles was kept in each jar.

Samples were taken every four hours, beginning the day collected. After the rows of teeth appeared to be well formed, the number of samples per day was reduced, ultimately to two. Samples of this series

were taken through May 15th. This series was designated as "B. f.-33-A." The series was supplemented by later collections.

On June 12th Dr. H. J. Van Cleave collected from the same pond from which the eggs were taken earlier a series of tadpoles and young toads. In body size of individuals this series overlapped considerably the series B. f.-33-A; and this series was designated as "B. f.-33-B."

On June 9th, 1934, the author collected a series of tadpoles from the same pond, the body sizes of individuals of which overlap the series B. f.-33-B, and attain the maximum size of tadpoles of the species. This series has been designated as "B. f.-34-A."

The tadpoles of all series of *B. fowleri* were preserved by the same method as that employed in the preservation of the tadpoles of *P. nigrita triseriata*.

It might be stated at this point that the only toads collected or observed over a period of several years anywhere in the vicinity of the pond from which the tadpoles of these series were taken have been *B. fowleri*.

In the actual study of the tadpoles the only selection of any kind exercised was one to secure as even a distribution of body size as possible. Obviously only tadpoles having some traces of rows of teeth and/or horny beaks were studied in detail.

Rana pipiens.—The eggs from which the tadpoles of this species were reared were collected on April 9, 1933 from a pool near Veedersburg, Indiana, by Dr. H. J. Van Cleave. There were two clutches of eggs; and the eggs of each were in all stages of gastrulation the morning of April 10th, when brought to the laboratory.

Samples were taken at intervals of not more than four hours from April 11th to April 23rd, and once or twice daily from the latter date through May 15th.

The tadpoles were reared in finger bowls in which were kept Elodea and algae. The diet of the tadpoles was supplemented with "Justrite" fish food. Beef and liver were not very readily eaten by tadpoles of *R. pipiens*, although offered to them frequently. Water in the finger bowls was kept fresh, and samples were taken from different bowls so as to maintain approximately the same number of tadpoles in each bowl.

The tadpoles of the two series of *R. pipiens* were preserved by the same method as that employed in the preservation of the tadpoles of the other species previously discussed.

Specimens from the preserved series were selected for detailed study, the selection being only to secure as even a distribution of body size as possible over the range of sizes included in the series. Too, only tadpoles with some traces of rows of teeth and/or horny beaks were studied in detail.

APPARATUS AND METHODS OF STUDY

After some "trial and error" the routine technique as described below was followed for all animals examined.

Apparatus.—All studies of animals were through the use of a dissecting binocular microscope. Illumination was from an adjustable spotlight ("Point-a-light"). All body measurements were taken with an ocular micrometer in a 10x ocular, with 55 mm. objective.

Drawings were made through the use of a camera lucida fitted on the dissecting binocular. Some difficulty was experienced in the preliminary attempts in securing uniform magnification in all drawings and in each drawing over the entire field of the microscope. An apparatus was, however, assembled to overcome this difficulty. An adjustable dissecting lens holder was secured. This lens holder had a heavy base, a long arm that could be bent to table level, and a screw adjustment similar to and with about the ratio of that on any ordinary microscope.

In place of the loop holding the lens and forming part of a universal joint there was inserted a ring support, of which the ring was about 10 cm. in diameter. On this ring a "stage" was securely fastened by means of comparatively fine wire. This stage was simply a heavy, layered piece of cardboard about 12 cm. square. Circles were cut from the center of the upper two of the three layers so as to form a "pit" in the center of the stage. These circles were of such a diameter as to exactly accommodate a Syracuse watch glass. Thus a watch glass could be turned in the circular pit thus formed on the stage but could not slip at all from side to side as the stage was placed at precarious angles. Further, this stage could be tilted at any angle and in any plane, and could be raised and lowered by means of the screw adjustment of the lens holder supporting it.

With this adjustable stage entirely apart from the dissecting binocular microscope, the microscope could be set at a fixed elevation, and the arm length and angle of the mirror of the camera lucida set at a fixed length and angle respectively. These "fixed" adjustments were such as to insure uniform magnification of the entire field and at all times, provided the object examined were at all points in sharp focus, to insure which latter involved tilting the adjustable stage so that the object examined would have its plane perpendicular to a line drawn through the axis of the objective used in making the camera lucida drawings.

10x oculars and 25 mm. objectives were used; and through use of a slide micrometer the above mentioned adjustments were so made as to make possible a drawing of a magnification of exactly 100 diameters. These adjustments, namely, the "elevation" of the microscope, the length of the arm and the angle of the mirror of the camera lucida, were not

disturbed throughout the making of the drawings, although the magnification was checked at frequent intervals. An exception was made in the case of the tadpoles of series B. f.-34-A. The large size of the mouthparts of these tadpoles forced substitution of the 40 mm. objective for the 25 mm. objective. The adjustments were reset to make possible drawings of the same magnification, i.e., 100 diameters, as were made throughout all series.

A Syracuse watch glass was thickly lined with paraffin. In the bottom of this paraffin-lined watch glass a somewhat funnel-shaped depression was made at such an angle so that when the tail of a tadpole, ventral side uppermost, was inserted in this depression, the mouthparts of the tadpole would be in the plane most facilitating study (cf. above). Very fine elbow insect pins were used to hold the tadpoles in place while drawings were being made. The "elbows" were inverted on the pins; and the pins could be inserted in the paraffin so that the "elbow" points rested sufficiently firmly on the tadpole to hold it in the most desirable position for study and drawing.

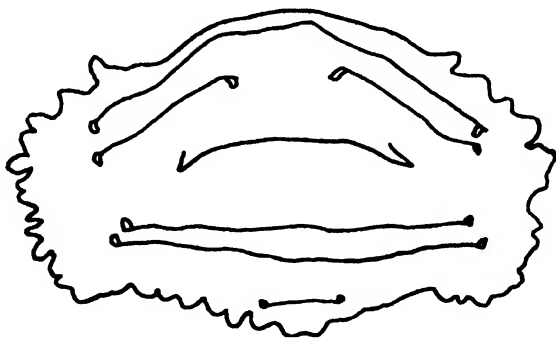


FIG. 2.—Camera lucida outline drawing of mouth parts shown in Fig. 1. This outline illustrates the type from which all measurements have been taken.

Drawings and Observations.—Outline drawings were made of the mouth apparatus of each tadpole selected as above described for each series. Each of these drawings was made as follows (cf. Fig. 2): An outline of the disc itself was made. Then a line was drawn along each row of teeth so as to follow the bases of the teeth. The end teeth in each row or part of a row were outlined so as to give more definite and exact terminations to the lines representing the rows. Teeth in unusual positions and teeth in irregular rows were also individually outlined. At the same time the outlines of the rows of teeth were drawn the number

of teeth in each row was determined. Counting the teeth in each row was in some instances rather tedious and difficult. However, no count was permanently recorded until the same number could be obtained in three successive counts. The upper and lower beaks were also outlined; and it was often necessary to change the focus (by adjustment of the stage) in order to have the ends of the upper beak clearly defined. This was usually done after the rows had been outlined and teeth had been counted.

Making such drawings had the advantage over taking direct measurements of being far less difficult with no loss, if not a gain, of accuracy, and forming a permanent and readily accessible record.

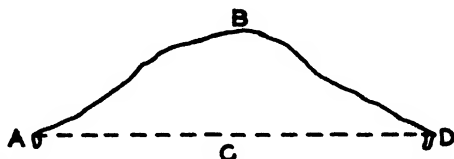


FIG. 3.—Outline of a single row of teeth to show difference between chord and arc lengths. Broken line, ACD, is chord length of row of teeth, ABD. Solid line, ABD, is arc length of row of teeth, ABD.

Measurements.—Since all drawings were made at a magnification of 100 diameters, the taking of measurements from the drawings was much simplified. A vernier caliper equipped with rather sharp divider points was used in taking the measurements from the drawings. The caliper read to tenths of millimeters; and, since magnification was 100 diameters, the measurements could be taken without interpolation or correction actually to thousandths of millimeters.

The measurements taken are all referable to the bases of the rows of teeth. The difference between the length of a row of teeth as measured from the bases of the terminal teeth and the length as measured from the tips of the terminal teeth might perhaps not be proportionately a significant difference in large tadpoles, but it is significantly large in smaller tadpoles.

Two different measurements of each row of teeth were taken (cf. Fig. 3). One of these measurements was the shortest distance between the ends of a given row. If a row of teeth were considered an arc, this measurement, i.e., the shortest distance between the ends of the row, would represent a chord subtending the arc. Accordingly, this measurement will hereafter be referred to as the "chord measurement" or "chord length" of a row. It was thought that the actual lengths of the rows

might show some correlations with body measurements that chord lengths would not show. Hence, the actual length of each row was measured. This measurement was taken with a cartometer, an instrument which could be rolled along the lines on the drawings, which lines were outlines of the rows of teeth. The cartometer used could be read to 1/32 inch. The vernier caliper used was graduated both to sixty-fourths of inches as well as to tenths of millimeters, and could therefore be used in very readily translating the cartometer readings into millimeters. The actual length of a row of teeth thus obtained will hereafter be referred to as the "arc measurement" or "arc length" of a given row.

The median space in the second upper row of teeth was also measured. The distance between the bases of the right and left parts of this row is the measurement used in the comparisons made in this study. However, since Wright (1929) makes no mention of exactly what criteria are used in determining the width of this space, the minimum distance between right and left parts was also taken, although in the course of the study this measurement proved more irregular. Differences between the two measurements might not be of any proportionate significance in large tadpoles; but in smaller ones the differences are proportionately large.

Both chord and arc lengths of the upper beak were also taken. Due, however, to the position of the beaks relative to the rows of teeth, the arc length of the upper beak as taken is perhaps without significance. The lower beak is hidden from view to a greater or lesser extent by the upper beak, and could thus not be measured.

The greatest width (laterally) of the oral disc was also taken, although the degree to which the papillary borders were curled inward was too irregular to permit this measurement as taken to be of reliable consequence.

A summary of the various measurements and counts made of the mouthparts may be given here. They are chord length, arc length, and number of teeth of each of the rows as follows; first upper, right part of the second upper, left part of the second upper, first lower, second lower, and third lower; chord length of the second upper row as a "unit" or single row; minimum width of the median space in the second upper row, and the width of the space as taken between the bases of the terminal (median) teeth of right and left parts; arc and chord lengths of the upper beak; width of the oral disc; and in some instances of irregularities the actual length of that part of a row actually bearing teeth.

In view of the possible correlations that might be found to exist the following body measurements were taken: (1) body length (tip of

snout to posterior border of anus), (2) tail length (anus to tail tip), (3) greatest body width, and (4) greatest body depth.

As the observations, body measurements, and drawings of each tadpole were completed, each tadpole was given a number and marked to maintain its identity in a given sample in event of possible need for re-investigation of individuals. The marking of the tadpoles consisted in clipping with very fine scissors V-shaped pieces from the upper and lower parts of the tail fin, the number given any tadpole being a fraction, the numerator and denominator of which indicated the number of pieces cut from the dorsal and ventral parts respectively of the tail fin.

Method of Analysis of Data.—Instead of calculating the ratio between two given measurements, e.g. the ratio of the chord length of one row to the chord length of another row, or the ratio of the arc length of a row to the chord length of the same row, such "pairs" of measurements from each animal of a series were plotted against each other graphically, or as coördinates. Lines of "equal proportion" were drawn on each such resulting graph. Any individual ratio could be determined by passing such a line of equal proportions (i.e., a line through zero) through the plotted point in question. The ordinate value of the point at which such a line passes through a point having a value of 1.00 on the axis of abscissas is the ratio to one that exists between the two coördinates (plotted measurements), determining the point through which the line of "equal proportions" has been drawn. The value, however, of this method of studying ratios between two sets of measurements is not particularly in the simplification of determining the ratios. The successive changes of ratio with increase in values of the measurements concerned, the minimum and maximum ratios, the variation of ratios, the trend of the majority of ratios, etc., are all at once obvious when measurements of two parts or two measurements of the same part are thus plotted as coördinates. Examples of the type of graph obtained and used in determining the ranges of ratios discussed later in this study are shown in Charts 1 to 8.

This graphic method of analysis was also used in studying the numbers of teeth in given rows as compared with the arc lengths of the rows (Chart 3).

The proportionate numbers of teeth in the different lengths of the corresponding row on different animals were readily compared on such graphs, and the actual number of teeth per unit length of row could be determined just as ratios between two measurements were determined (cf. above). This method applied to the study of tooth numbers has the same advantages that the method has in a study of ratios.

ANALYSIS AND DISCUSSION OF RESULTS

Bufo fowleri

DESCRIPTION AND ANALYSIS OF THE MOUTH PARTS

General Features.—The disposition of the rows of teeth are the same in *B. fowleri* as in the common type described in the introduction (pages 2-4).

The upper beak appears (becomes heavily pigmented) before the presence of any teeth can be detected. Teeth first become apparent in the first upper row, but only very shortly before teeth appear in the other rows. In some instances teeth of the second upper row appear shortly after teeth appear in the first upper row and before teeth appear in any other row. In all except some of the largest animals examined teeth are present in each lower row if present in any. In no instance in younger tadpoles is any row of teeth complete before at least some teeth of the other rows have appeared. However, those rows in which teeth first appear are usually the rows to first become complete. The row first complete, if any, in a given case is the first upper row.

The only rows developing any general irregularities or variations are the first and second lower rows. These variations or irregularities, if such these changes may be called, are divisions of a row into two or more parts, with spaces of varying widths separating the parts.

The first lower row is divided in almost half of the tadpoles examined. In half of the instances in which there are divisions, the division of this row is into two equal parts without an appreciable space, if any, developing between the right and left parts. Such an appreciable space is not greater than the width of one or two teeth. The two parts in the case of such a division tend to take the shapes of arcs of smaller, separate circles, rather than remaining as separate parts of the same arc. This will be further discussed later. If the row is divided into two unequal parts or into more than two parts, the parts are usually somewhat separated, and remain more as arcs of the same circle. In the smallest animals in which the row has been fully formed, it is undivided. In slightly larger animals it is irregularly divided. And in still larger animals the row tends to be divided into two regular parts (as described above). In the largest animals the row is rarely divided in any other way than into two equal, unseparated parts. Such a division occurs in about one-fourth of the largest animals.

The second lower row is divided in about one-sixth of the animals studied. In about one-third of these cases, division is into two approximately equal parts. In the other of the cases the divisions may be into as many as four parts. The same general sequence of divisions with

increase in size occurs in this row as in the first upper row. However, divisions of any kind of the second upper row are rare.

There are no other rows in which changes are quite so frequent. In about 6% of the animals examined the first upper row is divided into two unequal parts which may be more or less separated. However, the parts do not assume the proportions of arcs of separate circles. In other rows irregularities are rare (1-2%).

When the rows of teeth disappear with the onset of the metamorphic climax, the third lower row disappears first, or at least begins to disappear first. The others disappear almost simultaneously, the first upper row being perhaps the last to disappear completely. The lower mandible disappears before the upper mandible. The mandibles apparently either disappear before the rows of teeth disappear or before the teeth disappear completely.

As was stated in the introduction, one of the objects of this study has been to determine whether or not there might be some basis for the possible existence of constant relationships between different parts of the mouth apparatus. Since the series of *Bufo fowleri* tadpoles includes individuals representing the entire size range of tadpoles of this species, it was decided to use the data from this series of tadpoles as the basis of an analysis of growth phenomena in the mouth apparatus; which analysis should discover or disprove some explainable basis justifying the use of relative measurements as taxonomic characters.

It was decided first to determine whether or not the various rows of teeth have regular or characteristic growth rates in relation to body size. There are several measurements of the body that might be used as a basis of comparison. Of these, body length was chosen as being the least affected by various conditions of preservation, amount of feeding prior to preservation, changes during early metamorphosis, and handling during study.

First Upper Row.—From examination of Chart 1 it will be seen that the curve representing the averages of this row of teeth is S-shaped. There are two possible explanations, namely, either there is a second acceleration of the rate of growth of the row as metamorphosis approaches, or the second upturn of the curve is due only to the larger tadpoles being of a different series. It is possible that these animals, due to different seasonal and other conditions, had not passed the period of greatest rate of growth of the row, although their size is greater. However, the data for the different groups overlap sufficiently to make this doubtful.

For the entire group the length of the row per 10 mm. of body length varies from 1.22 mm. to 2.60 mm. (cf. Table I). Exclusive of what appear to be extremely irregular or unusual cases, the variation is

from 1.45 to 2.38 mm. per 10 mm. of body length. The average length varies between 1.45 and 2.13 mm. per 10 mm. of body length. Omitting the smaller animals in which the row is not fully formed, the first and last averages are about equal per unit length of body. Although the actual length of the row varies between wider limits in larger animals, the length per unit body length varies less.

Since the arc length of the row may more nearly approximate its actual "value" as a growing part, this length was plotted against body length to determine whether some more definite relation might obtain. The curve is of the same general contour as that of chord length/body length. The actual variation in arc length of the row per a given body

TABLE I.—*Bufo fowleri*: CHORD LENGTHS (IN MM.) OF MOUTH PARTS PER 10 MM. OF BODY LENGTH

Row	Minimum	Maximum
First upper.....	1.22	2.60
Average of right and left parts of second upper..	0.35	1.09
First lower.....	1.24	2.20
Second lower.....	0.68	2.00
Third lower.....	0.80	2.00
Upper beak.....	0.90	1.53

length may be noted to be greater in larger animals. However, the variation per unit of body length is no greater, if as great, until shedding of the teeth begins (the teeth appear to be shed irregularly in short groups). The actual variation of row length per 10 mm. body length is also greater as compared with chord lengths for the group as a whole.

Now, if the chord length be plotted against the length of body plus tail a much smoother curve of averages is obtained. However, the variation of length of row per unit of total length of body plus tail varies just as much as it does per unit of body (only) length.

When arc length of the row is plotted against length of body plus tail, this arc row length per unit of body plus tail length is seen to vary slightly less as compared to its length per unit body (only) length. A very smooth curve of averages is obtained and the data are grouped about this curve with apparently less general variation than in the other combinations tried. This is taken to indicate that in this comparison exists a condition more nearly approximating one of relative growth.

As metamorphosis progresses the relation becomes more irregular. This is due most likely to irregularities both in row and in total body length which do not vary similarly, as in earlier instances. In the case of the latter the irregularity is apparently primarily a result of irregularity in tail length, since row length varies in these cases more per unit of

total length than per unit of body (only) length. This is to be expected, particularly when autolysis of the tail begins.

It also indicates that whatever conditions may affect tail length must also affect the length of the row of teeth. Thus, since total length includes a variable governed by conditions similar to or the same as those affecting row length, row length has a more nearly regular relation to total length than to body length alone, until the climax of metamorphosis approaches.

Number of teeth in the row is more irregular per unit of body length or of total length than are either chord or arc lengths, although it was thought probable that number of teeth might be more constant or regular per unit of body length. Number of teeth per 10 mm. of body length varies from 64 to 176, and per 20 mm. of total length from 53 to 158. For a given total length, e.g., between 284 and 290 mm., number of teeth may vary from 53 to 84 per 20 mm. of total length, or, actually, from 76 to 117. (Also, e.g., from 75 to 156 per 20 mm. total length at 8.5-9.5 mm. total length, or, actually, from 32 to 75.) Thus, it is obvious that number of teeth per row is not at all constant nor does it increase regularly per unit body or total length, although there is a general actual increase as growth proceeds.

Although it is desirable to determine just what unit or character of measurement of a row bears the more nearly "characteristic" growth relation to the body, it is not primary for the purpose at hand. Regardless of the measurement used or relation obtained, if two or more rows are found to be similar in such relations, it follows that such rows would in turn be comparable. Also, if certain irregularities in the rows are referable to differences in the different samples constituting the series, this, too, would be of no unfavorable consequence. It would rather determine whether all rows were relatively equally affected by the diverse conditions. Thus, the object of this portion of the study is ultimately to qualify rows for comparison.

Second Upper Row.—This row, being divided, might be considered either as a single row or as two separate rows. Is each portion to be considered a single growing part, or are the right and left parts fractions of one unit? If considered as one row or one unit, there are four instead of two ends from which lengthening may occur. Thus, if growth should occur equally at all points and the row grow actually as much as the others, the proportionate increase of its chord length as compared with those of other rows would be less. If each part be considered a separate row, and if each increases in proportion to its original size, increase in length of the row as a unit should still be less than that of other rows. (This, of course, presupposes that increase in length of a row is a constant fraction of the sum of growth complexes of the row.) Moreover,

it can be determined whether or not the median space between right and left portions is encroached upon by the growth of either of these portions. If not, then growth might be assumed to occur only at the outer ends of each of the parts. Should this be the case, it is to be expected that the outer ends extend twice as rapidly in proportion to row length as do the other rows. If the median space is encroached upon by growth of right and left parts, it might be expected that the outer ends of the rows would increase only in proportion to original row length. This would mean that the ends of the first upper labial row would extend progressively further beyond the outer ends of the right and left parts of the second row. The same would be expected if the second row were considered as a unit. If increase in length, as already presupposed, be a constant fraction of the entire complex of growth of a row, and if rate of growth is proportional to original size, then the first upper row should increase in length more rapidly than the second upper row. Thus, if these two rows are compared graphically by plotting the length of the first against that of the second, the curve obtained should show an increasing ratio. Such, however, is not the case. The chord lengths, whose relation to arc lengths will be discussed later, remain within limited ratios, namely, between a ratio of 0.90/1.00 and one of 1.25/1.00 with a nearly constant average of slightly more than 1/1. Unraveling the premises of the above assumptions, it will be seen that increase in length of a row is not a constant fraction of total proportionate growth of the row.

The median space in the second row is not obliterated and does not become actually smaller, but it does become a progressively smaller fraction of the row as a whole. This must mean that, as the space itself grows, the right and left parts of the row grow into the space at a rate slightly less than that at which the space increases. Thus, the right and left parts do grow at each end and yet the outer ends continue to grow as rapidly as those of the first upper row, which has only two points of lengthening. This, then, lends support to the idea that increase in length of a row is not a constant fraction of total proportionate growth of the row. It seems likely that each end of any row advances at a rate that is independent of what may be occurring in other parts of the row, although all the processes may be affected and similarly, by the same factors.

It must also be borne in mind that the entire disc is enlarging, and relative points on the disc are being diverged along radii, perhaps unequal and disproportionate. A row may be considered an arc from a circle whose radius is increasing with the center as a fixed point. The arc, then, is forced peripherally and must "stretch" to meet the "demands" of an increased circumference. This "stretching" is apparently brought about by cell division in the plane of the radius and at right angles to the surface of the disc. Teeth may be observed to "split" from the base

outward, indicating that a cell division in such a plane has occurred. Thus, the increase in length of a row appears reduced to the result of two processes; namely, the ends of the row are carried apart by the growth of the disc, being "ideally" pushed outward in straight lines by the lengthening radii, and the ends of the arc at the same time are themselves moving further around the circumference. These two processes are perhaps fundamentally similar, yet in the first the already formed ridge is lengthening, while, in the second new material is being added to it. At any rate, it seems that the advance of the ends around the circumference would occur independently of the other process. This may be determined experimentally.

Furthermore, if the percentage increase in length of the first upper row and that of the second upper row be plotted against actual increase in length of the body, it may be seen that, although the two curves have similar contours, they are widely divergent. This is true both in the percentage increase over original size and in percentage increase over each preceding increase.

Aside from showing two periods of growth, this adduces proof that the different rows of teeth are similarly affected by the various conditions of growth, but that the responses of the various rows is not to be measured in constant fractions of their original lengths.

By comparing the percentage increases in the average lengths of right and left portions of the second upper row with the percentage increase in width of the median space, it will be seen that the increases in the two dimensions concerned are reciprocally correlated. This indicates that when the rows are lengthening at their greatest rates, the median space is broadening more slowly, due to the rapid encroaching of the inner ends of the rows. It is possible that the entire disc, of which the "median space" is only a portion, may enlarge at a fairly constant rate, while the rows of teeth increase in length in "spurts." Thus, what appear to be periods of "negative growth" of the median space are only periods during which the rows of teeth are growing faster than the space. When the rate of growth of rows of teeth drops, the space appears to broaden more rapidly. All this lends further proof to the apparent fact that the ends of the rows of teeth encroach upon the circumferences, of which they are arcs, rather independently of other growth processes concerning the disc.

First Lower Row.—When the chord length of the first lower labial row is plotted against body length, the same type of curve results as in the case of the upper rows. The variation in length of row per 10 mm. of body length is from 0.77 to 2.18 (omitting cases where part of row is missing). Excluding very young and exceptional cases (less than 5%

of total) the variation is from 1.24 to 2.03 mm. per 10 mm. of body length, with the rows of teeth of the smallest and of the largest animals nearer the lower limit of this range.

A curve showing average percentage increase in length of the row has similar contours to those of the rows previously studied; but it varies somewhat from them in actual percentages.

Second Lower Row.—Because this row appeared to be subjected to less irregularities than the first or third lower rows of teeth, it was chosen as the lower row for more complete comparison with body size. Chord length, arc length, and number of teeth were each plotted against body length. In each instance the same type of curve is obtained, namely, the same S-shaped curve as in the cases of other rows. Per 10 mm. of body length, chord length of the row varies between 0.68 and 2.00 mm.; arc length varies between 0.80 and 2.15 mm.; and number of teeth in a row varies between 49 and 122. One point of possible note about this row is that when number of teeth in the row is plotted against body length, the points on the graph representing the 1934 collection of tadpoles form such a distinct group that it indicates the probability that the characteristic second upturn of the curves of relative growth in this series is due to different conditions of growth of the sample rather than being a second growth period (as was discussed earlier).

Third Lower Row.—The chord length of this row, when plotted against body length, gives a curve similar to that of the other rows. The curve of percentage increase is also similar to those of other rows, although its modes are higher than those of the other complete rows.

Upper Beak.—Although the upper and lower parts of the horny beak are quite different from the rows of teeth, at least the upper part, when plotted against body length, shows a similar course of growth to that of the rows of teeth. Percentage increase is also similar, and the curve of this percentage follows very closely those of the first upper and first and second lower rows, both in contours and in actual percentage values. Per 10 mm. body length the upper beak varies in chord length between 0.90 and 1.53 mm. (exclusive of a few instances of tadpoles whose beaks could not be satisfactorily measured because of mechanical damage caused while making other measurements and counts.

Curvature of the Rows of Teeth.—From a study of the curvature of the rows of teeth, that is, the relation of arc to chord lengths (cf. Chart 2), several facts can be determined. It has been seen that arc length is a more true measure of the row as a growing part. If the same ratio between arc and chord measurements obtains throughout the series, or, if the ratio undergoes the same modifications in all rows, the use of chord lengths in comparisons between rows may be justified.

If, in any given circle, arcs of different lengths are plotted against the respective chords subtending them, it will be seen that the ratio between arc and chord increases as their lengths increase, first slowly and then rapidly until the greatest chord (the diameter) is reached. If a single straight line (other than diameter) is drawn through several concentric circles, and the lengths of the arcs and chords thus formed be compared, it will be found that the ratio between arc and chord length increases from smaller to larger circles. If non-concentric circles of different radii be so drawn that a single chord subtends an arc on each circle, it will be obvious that the ratio of arc length to chord length will be greatest in the smallest circles and least in the largest circles. If in concentric circles two radii be so drawn as to form any given angle, and chords be drawn from one radius to the other at the respective points at which they intersect the circles, the arc/chord ratios will in each case be the same. It follows, then, if for the moment a row of teeth be considered an arc of a "perfect" circle, that, if the increase in length of a row of teeth were due only to the expansion of the disc along its radii, the ratio of arc to chord length would remain the same. If, however, the ends of a row should grow around the circumference so as to extend the arc to points representing projections of the original chord, or to any distance beyond the original radii, then the ratio of arc to chord length will increase. Thus, an increase in arc/chord ratio of a given row would verify the idea that the row grows circumferentially at the same time the disc is expanding and 'over and above' this disc growth.

It must be remembered, however, that in most instances the rows of teeth are probably not arcs of "perfect circles" and that the different radii of the disc do not increase uniformly; and that irregularities in outline as well as differences in curvature, and differences in proportion of circumference concerned will affect the arc/chord ratio. Thus, an exceptionally high ratio would more than likely indicate a row with a wavy outline.

From examination of Table II and Chart 2 it will be seen that there is, in the case of each row, a slight increase in curvature from smaller to longer rows, both as to averages and as to actual least and greatest rows. The greatest arc/chord ratios are to be found in the case of the first upper row. This might be expected since this row is an arc of a greater circle, and also since it follows closely the margin of the disc and thus is more nearly a true arc than the other more centrally located rows, which are somewhat "flattened" in outline. This flattening is perhaps due either to unequal increase of the different radii of the disc or to failure of the rows to maintain a circumferential growth, or, more likely, to both. The third lower row, as expected, is quite similar to the first

upper row in arc/chord ratio, although the maximum ratio of not unusual cases does not reach as high a value, due to the fact that the third lower row does not ever attain the length of the first upper row.

If the three lower rows be compared, it will be seen that the arc/chord ratios increase from central to peripheral rows, indicating an increase in curvature of peripheral over more central rows. This is in accord with the above discussion, and shows the apparent existence of a sort of radial gradient that perhaps might be expressed mathematically in a manner similar to the "logarithmic spiral" expressing growth in such structures as the horns of the rhinoceros (Huxley 1932: pp. 151-154).

TABLE II.—*Bufo fowleri*: RATIOS TO ONE OF ARC LENGTH/CHORD LENGTH OF ROWS OF TEETH

Row	Maximum (all included)	Maximum (less extremes)	Row of least chord length	Row of greatest chord length	Approximate average in younger animals	Approximate average in older animals
First upper.....	1.32	1.21	1.00	1.21	1.06	1.16
Right part of second upper.....	1.22	1.11	1.00	1.11	1.03-	1.035
Left part of second upper.....	1.27	1.10	1.00	1.08	1.03	1.04-
First lower.....	1.14	1.10	1.00	1.05-	1.03	1.035
Second lower.....	1.17	1.12	1.00	1.08	1.035	1.055
Third lower.....	1.55	1.13	1.00	1.13	1.03	1.085

The portions of the second upper row might be expected never to develop as high arc/chord ratios as other rows, due to their being proportionately much smaller arcs, i.e., arcs representing a lesser percentage of circumference. However, the ratios are comparable with those of the first and second lower rows. This suggests that each row represents an arc of a circle with a center different from that of the other. Moreover, the outline of the first lower row tends to become emarginate with increase in length. In such instances the arc/chord ratio tends to become a ratio between the sums of two small arcs and two small chords and would thus be of a lesser value. This occasionally happens in the second lower row, but is much less frequent and much less marked. All this indicates the probable existence of at least two centers of expansion of the disc, which centers themselves move apart with growth. The expansion from these two centers must become less individual and merge to give a smoother contour as the periphery is approached.

Aside from the above, the first upper row is more similar to the third lower row than to any of the others in curvature and progressive changes

of curvature. The other rows are quite similar to each other. It follows that comparisons of chord lengths within these combinations might be expected to be more valid, provided chord lengths of the rows increase similarly. But chord lengths of the first upper and first and second lower rows increase at more nearly the same rates, while those of the parts of the second upper and of the third lower rows are more nearly alike. From this it must be concluded that the differences in rate of increase of arc length and in changes of curvature so interdigitate or counter-balance each other in the case of the first upper and first and second lower rows that the resulting chord lengths are quite comparable. The same appears to be true to less extent of the parts of the second upper and of the third lower rows. If the percentage increase of arc length per unit increase of body length in the cases of the different rows be compared, it will be seen that, as in the case of chord lengths, the curves have corresponding contours, but are actually of different values. The values probably are not of significant differences, however, between the first upper and first and second lower rows.

Numbers of Teeth in the Different Rows of Teeth.—It was thought that possibly the numbers of teeth in different rows might serve as a more reliable basis than measurements for computing ratios between rows. Hence, the first step in deciding the reliability of ratios between teeth counts was to compare the number of teeth to the arc length in each of the rows.

This was done by plotting the arc lengths against the numbers of teeth in the case of each row (cf. Chart 3). From the graphs thus obtained the numbers of teeth for every tenth mm. of arc length were averaged, and from these averages the number of teeth per 1 mm. of arc length for each average was determined, and plotted against arc length.

Examination of Chart 3 and Table III will show the results. Table III shows the maximum and minimum numbers of teeth per 1 mm. of arc length for each row. The difference between maximum and minimum is in almost each case very nearly 100% of the minimum number. The maximum and minimum numbers in the different rows do not appear to be significantly different in view of such variation. Obviously, the actual number of teeth in a row tends to increase as the row increases in length. But these increases do not seem to occur at coincident rates for the group of animals as a whole. The number of teeth per unit arc length will give a 'fairer' basis of comparison.

From examination of Chart 3 and Table III it will be seen that the number of teeth per unit arc length in any given row is at first small, then increases rapidly, remains at a given value (irregularly) for a while, then diminishes gradually, and then perhaps remains constant

until loss of teeth begins. By comparing the different rows in this respect, it will be seen that these variations occur simultaneously in all rows and irrespectively of the actual length of the row concerned. It may also be noted that numbers of teeth per unit arc length are approximately the same in smallest and largest animals. The initial low number may readily be explained as due to the fact that all the teeth in a given row in such a case have not become sufficiently deeply pigmented to be seen. Even, however, after all teeth are completely pigmented, there

TABLE III.—*Bufo fowleri*: NUMBER OF TEETH PER 1 MM. OF ARC LENGTH OF ROW OF TEETH

Row	Maximum	Minimum	Range
First upper.....	82	37	45
Right part of second upper....	74	35	39
Left part of second upper.....	78	30	40
First lower*.....	76	36	40
Second lower.....	72	40	32
Third lower.....	80	40	40

*This row is so much divided, often with spaces between divisions, that actual length of tooth-bearing portion is used here.

appears to be a further increase in number of teeth per unit arc length. The maximum is, however, reached comparatively early. Since each tooth is derived from a single cell or single column of cells (cf. earlier discussion), unless the teeth become somewhat separated from each other, which they appear not to do, it appears that the size of the teeth and tooth-producing cells must gradually increase with size.

The primary concern in this study, however, is the similarity in variation of tooth numbers in the different rows. From the variation of actual numbers per 1 mm. of arc length it does not appear that ratios between tooth numbers of different rows would be constant. Yet, from the similarity in different rows of variation of average number of teeth per unit arc length, it appears that tooth numbers might be of value as a basis of calculating ratios between rows. The determination of the actual value of these ratios must await comparison of rows through all methods of measuring (cf. later discussion).

INDICATIONS FROM THE ANALYSES

Presuming all rows to develop regularly (which they do not) and knowing (1) that the shorter rows have a greater percentage growth (due to the fact that the ends of any row extend themselves independently of the "size" of the row), and (2) that the rows nearer the

periphery develop the greatest curvature, it may be predicted that (1) the greatest range of ratios will exist between the longer and the shorter rows, (2) the ratios in older animals decreasing in general (if calculated as longer row to shorter row); (3) this range will be less and (4) there will be less difference between ratios in old and young animals, if the longer and shorter rows are both peripheral; (5) if the shorter row only is peripheral, the range will still be greater and there will be a greater decrease in ratio with age; (6) ratios between two longer rows (including use of the chord length of a divided row) are apt to be least variable, and (7) if one of these longer rows is a peripheral row, the ratio of peripheral row to a more central row will decrease slightly in older animals (since percentage arc increase is about the same in each, and since arc/chord ratio increases more in peripheral rows); arc ratios in such cases would increase correspondingly; (8) most constant ratios will exist between rows of more nearly equal length and of more nearly corresponding distances from the center or periphery of the disc; (9) ratios between the right or left parts to the separating space of a broken row will vary a great deal, increasing markedly with age. It might be further observed that the use of chord lengths instead of arc lengths is preferable in calculating ratios. Aside from their impracticability, arc lengths are of less value because (1) such ratios between arc lengths are more apt to vary with age, and (2) this greater variation tends to be counteracted by correspondingly increased curvatures if chord lengths are used.

Tooth numbers are (as has been previously observed) of uncertain predictable value. Their valuation must await actual comparison with other means of determining ratios, i.e., through use of arc and chord lengths.

To put these predictions into more concrete terms: (1) Fairly constant ratios may be expected between the first upper row and the first and second lower rows, particularly the second lower row. These may, however, decrease slightly with age. (2) Even more nearly constant ratios may exist between the second upper row (as *one* row) and the first and second lower rows, particularly the first lower row, (since the second upper and first lower rows are correspondingly disposed with respect to the center of the disc, and since the first lower also has a tendency to become two smaller rows (cf. also earlier discussion). There should also be some tendency for these ratios to decrease with age. (3) There should also be constant ratios between the two upper rows (second upper as *one*), the ratio approaching more regularly a 1/1 ratio with age. (4) The ratio of the first lower to second lower row will be rather constant. (5) The ratio of any other row to the average of right and left parts of the second upper row may vary more than any of the ratios

suggested above. The least variable ratio in this group would perhaps be that between the third lower row and the average of the parts of the second upper. (6) The ratio of the first upper to the third lower row may also be quite variable, but should change little with age. (7) The ratios between the parts, space, etc., of the second upper row will be of different constancies. (a) The ratio of the average of right and left parts to the median space should be extremely variable. (b) The ratio between the length of the row as a unit and the median space will also be extremely variable, though possibly less so than the former (a). (c) The ratio of the length of the row as a unit to the average length of right and left parts should be much more constant and a better means of expressing the extent of the median space.

It must be remembered, however, that these are only predictions made on the premises of the foregoing analyses, and the actual comparative values of the different combinations must be verified or disproved by the actual comparison of the rows in the various possible combinations. The value of these analyses, then, lies in the fact that, without being prejudiced by a knowledge of the variation or constancy of the different ratios, the ratios, should they fulfill predictions, shall have been shown to have a basis referable to certain rules and reasoning rather than such ratios being mere coincidents or artifacts.

COMPARISON OF RATIOS OF DIFFERENT ROWS OF TEETH TO UPPER BEAK

From a study of the percentage increases of the rows of teeth and the upper beak it was seen that the upper beak increases in chord length at a rate quite comparable to that of some of the rows of teeth, namely, the first upper and first and second lower rows, the former of these in particular. This suggests that a fairly constant ratio of chord lengths between any of these rows and the upper beak might obtain.

Of the nine different combinations of rows, etc., used by Wright in his key (Wright 1929), five of them concern the relation of rows of teeth to the upper beak (cf. also earlier discussion). All rows are used at various times except the right and left parts of the second upper row. For this divided row he uses the chord length as though the row were complete and single, i.e., the straight distance between the outer ends of right and left parts of the row. This measurement will hereafter be designated as the chord length of the second upper row. When right or left parts of the row are used, they will be designated as right and left parts.

Table IV is a summary of the results of plotting the chord lengths of the various rows against the chord length of the upper beak (cf. also Chart 4). All values (except percentages) expressed in the table rep-

TABLE IV.—*Bufo fowleri*: RATIOS TO ONE OF ROWS OF TEETH TO UPPER BEAK

Row	Extreme range			Restricted range			% Variation	Range of averages			% Variation	Approximate general average
	Minimum	Maximum	Amount	Minimum	Maximum	Amount		Minimum	Maximum	Amount		
First upper.....	1.18	2.06	0.88	1.48	1.94	0.44	30.0	1.60	1.72	0.12	3.6	1.60
Second upper.....	1.18	1.92	0.74	1.35	1.80	0.45	33.3	1.35	1.65	0.30	19.4	1.55
First lower.....	0.80	1.62	0.82	1.17	1.62	0.45	38.4	1.20	1.56	0.36	26.1	1.40
Second lower.....	0.70	1.64	0.94	1.10	1.56	0.46	42.0	1.23	1.44	0.21	7.9	1.35
Third lower.....	0.54	1.40	0.86	0.80	1.33	0.53	66.3	0.56	1.27	0.71	39.1	1.05
Average of right and left parts of second upper.....	0.33	0.82	0.49	0.50	0.79	0.29	58.0	0.94	1.44	0.50	21.0	None

rent ratios to one. "Extreme range" includes ratios of all cases in which measurements of both parts concerned could be taken. "Restricted range" does not include ratios of (1) cases of smaller animals where row or beak was too faint to be satisfactorily measured, or (2) obviously exceptional or irregular cases. The omitted cases in no instance constitute more than 3-5% of the total number of animals in the series under consideration. "Amount of range" refers to range of ratio, and is the difference between the maximum and minimum ratios of a given combination. The values under "percentage variation of restricted range" are expressed in the percentages of the minimum ratios of the "restricted ranges" that the ratios may vary in a given combination. The value of the use of these percentages lies in the fact that they give a basis of comparison of the different combinations which takes into account the differences in lengths of the rows in the different combinations. Thus, for example, a difference of .50 between .50 and 1.00 is an entirely different value than a difference of .50 between 1.50 and 2.00 "Range of averages" represents the range of averaged ratios. "Amount of range of averages" is the difference between maximum and minimum averaged ratios. "Approximate general average" is the ratio represented by a line on the graph concerned, so drawn as to pass through the greatest number of "average" points or to divide these points into two approximately equal groups. The values under "percentage variation of average" are given in percentages. They represent in percentage of the "approximate average" the amount that any average may vary either above or below the "approximate average," which is actually an "average of averages." Although the percentages refer to averages rather than to actual range, this is of value because it takes into account the distribution of the majority of cases.

By examination of Table IV and Chart 4 the constancy, value, and validity of these various combinations may be compared.

In order of *amount of extreme range* of ratios to upper beak from least to greatest the rows are respectively, (1) second upper, (2) first lower, (3) third lower, (4) first upper, and (5) second lower. If exceptional or extremely irregular instances are disregarded (not to exceed 3-5% of total number) in each case, the order of the rows from least to greatest range of ratios to upper beak will be (1) first upper, (2) second upper and first lower, (3) second lower, (4) third lower. The differences between the amounts of range do not appear significant in the latter comparison, except for the third lower row, which has a considerably greater range. The other rows have approximately the same ranges. Thus, excluding the unusual ratios in the case of each row, it appears that, with the exception of the third lower row, comparisons between the respective different rows and the upper beak appear to be

of equal validity and constancy. However, if this amount of restricted range be considered as a percentage of the minimum ratio in this range in each combination, the different combinations will be represented in a more true perspective. The rows in order from least percentage variation to greatest percentage variation of restricted range of ratios to the upper beak are (1) first upper, (2) second upper, (3) first lower, (4) second lower, and (5) third lower.

However, if the amount of range of *averages* be considered, it will be seen that the ranges of ratios discussed above are much more regularly distributed in some combinations than in others. The order of the rows from least to greatest amount of range of average ratios is (1) first upper, (2) second lower, (3) second upper, (4) first lower, (5) average of right and left parts of second upper, and (6) third lower. If percentage variation of the averages be considered, this same order will be seen to exist, but the differences between the rows appear exaggerated although they are shown in a more true perspective.

From the standpoint of the criteria combined, and to summarize the foregoing it may be said that, as was more or less anticipated from preliminary analyses, the following sequence is the order of value of the rows that have any value as concerns the constancy of ratio of their chord lengths to those of the upper beak: (1) first upper, (2) second upper, (3) second lower, (4) first lower—the first upper being of most distinctive merit as affording a constant ratio to the upper beak.

ACTUAL TEST OF RELATIVE VALUES OF DIFFERENT COMBINATIONS OF ROWS OF TEETH

Each possible combination of the rows of teeth was determined and a graph of each possible combination was made by plotting the chord lengths of the longer row as ordinates and the chord lengths of the shorter row as abscissae in each instance in which a constant difference in length was obvious (cf. charts 5 and 6). Similar graphs were made of the combinations of measurements of the parts and spaces of the second upper row. On each of these graphs lines representing ratios (lines through "zero") were drawn in pairs (1) so as to include all points, (2) so as to include all but rather irregular or extreme cases (not excluding over 3-5% of total number of animals in the series), and (3) so as necessarily to include only those points representing older animals. The spaces bounded by these pairs of lines represent respectively (1) the "extreme range"—or variation—of ratios, (2) what has been designated for the sake of convenience as "restricted range" of ratios, and (3) range of ratios in "older" animals.

In several instances averages were calculated, but lines drawn as nearly as possible through averages failed to pass through zero, indicating a change of average ratio. Since the combinations are so diverse and since the average ratios change considerably, it was decided not to use averages in comparing the values of the different combinations.

The three sets of "ranges" may be interpreted so as to determine, in addition to the facts their titles indicate, (1) whether the ratio of a given combination is greatest or least in younger or older animals, (2) whether the range of ratio is greater in younger or older animals, and (3) whether there is a tendency for the ratio to shift upward or downward with increase in age.

The "restricted ranges" were taken as a basis of more critical comparisons, since extreme cases are frequently quite isolated, and since this study was not primarily concerned with exceptional cases. Too, these exceptional cases are more often those of younger animals with rows of teeth not completely formed. And even when an older animal has an exceptional ratio, it would be "unfair" to take this exceptional instance as a "characteristic" upper or lower limit of the range of the ratio in question. As a basis of comparison that would take into account the proportion of the range of ratio a percentage value was calculated for the restricted range. This percentage value is the percentage of the median ratio of the restricted range that the range extends above or below this median. (1) This percentage value, (2) the limits of the "extreme range," (3) the actual amount of the extreme range, (4) the limits of the "restricted range," (5) the actual amount of the restricted range, (6) the limits of the range of older animals, (7) the actual amount of this range, and (8) the approximate relative size of the animals with the extreme ratios for each combination of rows are shown in Table V.

In Table VI are listed the combinations of rows used and in respective columns opposite these combinations are listed the relative numerical orders from least to greatest under and according to each of the criteria used.

As criteria for determining the relative value of each combination, the following were used: (1) the percentage variation of restricted range, (2) amount of restricted range, (3) amount of extreme range, (4) amount of range in older animals, and (5) various combinations of (1), (2), (3), and (4). The "final assigned rank" was assigned only after careful analysis of each combination according to these criteria.

Foregoing any discussion of the relative merits of individual combinations, the study of the ratios of the various combinations of rows in *B. fowleri* may be summarized by stating that evaluation, as carried out on the basis of the criteria set forth, of combinations for constancy

TABLE V.—*Bufo fowleri*: RANGES OF RATIOS OF DIFFERENT COMBINATIONS OF ROWS OF TEETH

Combinations	Extreme range			Restricted range			Range in older animals			Relative "ages" of	
	Maximum	Minimum	Amount	Maximum	Minimum	Amount	Maximum	Minimum	Amount	Maximum	Minimum
1 U/r & 1.....	5.55	2.20	3.35	4.20	2.18	2.02	2.92	2.20	0.72	Y	vO
1 U/2 U.....	1.25	0.90	0.35	1.22	0.98	0.24	1.12	0.95	0.17	vY	M
1 U/1 L.....	1.60	0.96	0.64	1.50	1.00	0.50	1.24	1.00	0.24	vY	M
1 U/2 L.....	1.74	0.97	0.77	1.48	1.06	0.42	1.33	1.09	0.24	vY	M
1 U/2 L*	1.60	1.00	0.60	1.52	1.06	0.46	1.57	1.05	0.52	M	M
1 U/2 L†	2.48	0.94	1.64	1.85	1.06	0.79	1.47	0.94	0.53	O-M	vY
1 U/3 L.....	4.04	1.10	2.94	2.22	1.30	0.92	2.22	1.18	1.04	Y	M
r & 1/m s.....	4.60	0.36	4.24	2.64	0.60	2.04	4.60	1.25	3.35	O	vY
2 U/r & 1.....	5.00	2.00	3.00	3.46	2.13	1.33	2.96	2.00	0.96	O	O
1 L/r & 1.....	4.36	1.52	2.84	3.24	1.79	1.45	2.52	1.79	0.73	Y	vY
2 L/r & 1.....	5.00	1.34	3.66	3.56	1.70	1.86	2.34	1.70	0.64	Y	vY
3 L/r & 1.....	3.12	0.92	2.20	2.18	1.21	0.97	1.94	1.09	0.85	vY	vY
2 U/m s.....	8.50	1.68	6.82	5.75	1.98	3.77	46.3	8.50	6.19	O	O
2 U/1 L.....	1.65	0.86	0.79	1.35	1.00	0.35	1.25	0.86	0.39	vY	Y
2 U/2 L.....	1.72	0.93	0.79	1.43	1.03	0.40	1.39	1.03	0.36	vY	Y
2 U/3 L.....	3.72	1.15	2.57	2.18	1.25	0.93	1.80	1.25	0.55	Y	M-O
1 L/2 L.....	1.25	0.81	0.44	1.22	0.88	0.34	1.22	0.96	0.26	Y	M
1 L/3 L.....	3.26	1.00	2.26	1.85	1.05	0.80	1.85	1.03	0.82	Y	M
2 L/3 L.....	3.46	0.96	2.50	1.80	1.06	0.74	1.64	1.00	0.64	Y	M

KEY

1 U is first upper row.

2 U is second upper row (as a "unit").

m s is median space in second upper row.

r & l is average of right and left parts of second upper row.

Ages: These relative ages, or perhaps more preferably, relative sizes, were determined by relative distance from "zero."

Y is young.

vY is very young.

M is medium.

O is older.

1 L is first lower row.

2 L is second lower row.

3 L is third lower row.

vO is very old.

and reliability of ratio seems to justify the following order of combinations of rows from greatest to least value: (1) first upper/second upper; (2) first lower/second lower; (3) second upper/first lower; (4) second upper/second lower; (5) first upper/second lower; (6) first upper/first lower; (7) first lower/third lower; (8) first upper/third lower; (9) second lower/third lower; (10) third lower/avg. parts second upper; (11) second upper/avg. parts second upper; (12) second upper/third lower; (13) first lower/avg. parts second upper; (14) first upper/avg. parts second upper; (15) second lower/avg. parts second upper; (16) avg. parts second upper/median space second upper; (17) second upper/median space second upper.

TABLE VI.—*Bufo fowleri*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE V.

Combinations of rows of teeth	Criteria				Final assigned rank
	Percentage variation of restricted range	Amount of restricted range	Amount of extreme range	Amount of range in older animals	
1 U/2 U.....	1	1	1	1	1
2 U/1 L.....	2	3	5	6	3
1 L/2 L.....	3	2	2	4	2
2 U/2 L.....	4	4	6	5	4
1 U/2 L.....	5	5	4	3	5
1 U/1 L.....	6	6	3	2	6
2 U/r&1.....	7	12	13	14	11
1 U/3 L.....	8	9	12	15	8
2 U/3 L.....	9	10	10	7	12
1 L/3 L.....	10	8	8	12	7
2 L/3 L.....	11	7	9	8	9
3 L/r&1.....	12	11	7	13	10
1 L/r&1.....	13	13	11	11	13
1 U/r&1.....	14	15	14	10	14
2 L/r&1.....	15	14	15	9	15
2 U/m s.....	16	17	17	17	17 (-16)
r & 1/m s.....	17	16	16	16	16 (-17)

Symbols used for rows are the same as in Table V.

If the values indicated by the preliminary analyses be compared with these assigned values, it may be noted that there is exact coincidence in the valuation of the first six combinations. The predicted and assigned values also coincide as to relative value within groups (as arranged in assigning values). It appears then, that if the series of *Bufo fowleri* tadpoles studied may be considered as representative of the species, the ratios existing between the different rows of teeth and between rows of teeth and upper beak are not chance ratios but are determined by the

phenomena of growth and variation in this species. It further appears that, though the length of rows per body or total length may vary under different conditions, the more valued ratios between rows are little, if at all, affected.

The ratios between rows as given in Table V may be said in part to characterize tadpoles of *B. fowleri*, though they may not prove to be individually distinctive. If the phenomena of growth may be presumed to be fundamentally similar in other species, such other species would be forced, indeed, to possess rows of teeth of different proportionate lengths if the ratios between rows are to be distinctive at all.

It may be further observed at this point that the combinations of rows having the more constant ratios are apt to be the ones less distinctive of the species. Hence, it does not follow that the relative values assigned to the different combinations of rows on the basis of constancy of ratio will coincide with the values of the combinations based on the degree to which they are distinctive of the species. These latter values await further study of and comparison with other species.

For the purpose of simplifying comparisons with other species the combinations of row with row and of row with upper beak may be evaluated as a single group and on the basis of the same criteria. When this is done it is found that the combinations involving the upper beak will rank in order immediately following the group of the first six ranking combinations of rows (p. 43) as follows: First upper row/upper beak, second upper row/upper beak, second lower row/upper beak, first lower row/upper beak, third lower row/upper beak. The rank of value then changes to the combination of rows and continues as listed (p. 43) with the only exception being that the rank of the combination, average of right and left parts of second upper row/upper beak, is probably intermediate between the combinations, second lower row/average of right and left parts of the second upper row, and average of right and left parts of second upper row/median space in second upper row, respectively. This evaluation of all combinations as a group will be summarized in comparative tables further on.

Pseudacris nigrita triseriata

DESCRIPTIONS OF THE PARTS OF THE MOUTH APPARATUS

When all rows of teeth have completed their appearance, the rows of teeth in *P. nigrita triseriata* have the same arrangement as the general type described in the introduction (cf. pp. 9-11 and Fig. 1).

The upper mandible becomes sufficiently darkened to be readily measured before any teeth appear. Teeth of the first upper row are generally the first to appear, followed shortly by those of the first and

second lower rows, and then those of the second upper row. No one of these rows is completely toothed before teeth of the other three have begun to appear. However, all of these rows are complete some time before the third lower row appears. All rows of teeth except the third lower row may be complete in tadpoles of as small a body length as 2.32 mm., while the third lower row may not appear until the tadpoles have attained a body length of 3.36 mm., and may not be completely toothed when body length is as great as 3.57 mm. However, traces of the third lower row may be seen in tadpoles whose body length is 2.91 mm. The possible significance of the late appearance of this third lower row will be discussed later.

Changes in rows and such division of rows as have been termed irregularities are not frequent in this species. Irregular divisions in any given row do not occur in more than 2-4% of all cases examined after such a given row has become completely toothed.

There is, however, a tendency for the first lower row to become divided so as to form two short rows which are not separated but which are arcs of different circles. Such a division occurs in about 12% of all cases examined, being about equally distributed between the medium-sized and larger tadpoles of the series. A similar division may occur in the second lower row in a few instances (2-3%).

CURVATURE OF THE ROWS OF TEETH

Table VII gives the ratios of arc length/chord length for the rows of teeth. Since the tadpoles of this series studied did not attain the maximum size of the species, it follows that, if arc length increases in relation to chord length throughout larval life, the ratios expressed in Table VII are not as great as might obtain in tadpoles larger than those involved in this study. However, the ratios in the series of *Pseudacris nigrita triseriata* studied are slightly greater than in *Bufo fowleri*. The

TABLE VII.—*Pseudacris nigrita triseriata*: RATIOS TO ONE OF ARC LENGTH/CHORD LENGTH OF ROWS OF TEETH

Row	Maximum (all included)	Maximum (less extremes)	Minimum
First upper.....	1.25	1.25	1.05
Right part of second upper...	1.29	1.15	1.00
Left part of second upper....	1.45	1.21	1.00
First lower.....	1.32	1.18	1.00
Second lower.....	1.62	1.28	1.00
Third lower.....	1.59	1.22	1.00

ratios differ less in tadpoles of different sizes than is the case with *B. fowleri*. That is, the general distribution of ratios does not show any notable change with increase in body size. This indicates then, that arc length/chord length ratios are in general greater in tadpoles of *Pseudacris nigrita triseriata* than in those of *Bufo fowleri*.

It may also be noted that there is a general increase in arc length/chord length ratio from the more central to the more peripheral rows of teeth. This was noted to be true also for *B. fowleri*.

NUMBERS OF TEETH IN DIFFERENT ROWS OF TEETH

Number of teeth per unit arc length of a given row of teeth does not appear to change with increase in body size as numbers of teeth per unit arc length of rows were seen to vary in *B. fowleri*. This, however, is true because of the fact that the series of *P. nigrita triseriata* does not include a complete range of body sizes.

However, number of teeth per unit arc length of a given row (cf. Table VIII) is almost as variable in *P. nigrita triseriata* as in *B. fowleri* (compare Tables III and VIII).

In general in *P. nigrita triseriata* the minimum numbers of teeth per unit arc length of the different rows are greater, indicating that the teeth may be smaller than in *B. fowleri*. However, maximum numbers of teeth per unit arc length of the rows are not so different in the two species, the numbers being somewhat greater in *P. nigrita triseriata*, indicating further that teeth may be smaller in this species.

The small minimum number of teeth in the case of the third lower is due to the fact that teeth in this row may be widely separated for some time, which fact is in turn because of the fact that some of the teeth are slow to appear. The high maximum number of teeth in this row indicates that the teeth of this row may be of a smaller extreme size than in the cases of the other rows.

TABLE VIII.—*Pseudacris nigrita triseriata*: NUMBER OF TEETH PER 1 MM. OF ARC LENGTH OF ROW OF TEETH

Row	Maximum	Minimum	Range
First upper.....	83	45	38
Right part of second upper...	82	42	40
Left part of second upper....	88	43	45
First lower.....	83	51	32
Second lower.....	79	42	37
Third lower.....	133	29	104

It may be stated finally, then, that numbers of teeth per unit arc lengths of rows of teeth are in general as variable in *Pseudacris nigrita triseriata* as in *Bufo fowleri*, even though the body sizes of the tadpoles of the former species are not of sufficient variation to show the changes in numbers of teeth per unit arc length of row with increase in size as are shown in the tadpoles of *Bufo fowleri* studied.

COMBINATIONS OF ROWS OF TEETH AND OF ROWS OF TEETH AND UPPER BEAK

The same criteria are used to determine the relative values of the ratios of the different combinations of rows and combinations of rows with upper horny beak in *Pseudacris* as were used in the similar studies on *Bufo fowleri*. These criteria are (1) amount of extreme range of ratio, (2) amount of "restricted" range of ratio, (3) percentage variation of restricted range, (4) amount of range of ratio in older animals, and (5) the "relation" of the range in older animals with restricted range.

Combinations Involving the Third Lower Row.—Before summarizing the relative values of the different combinations, special attention may be directed to the combinations involving the third lower row. Since in plotting the four combinations involving the third lower row the latter was plotted along the axis of abscissas in each instance (as also cited above), it follows that the maximum extreme ratio is in each instance infinity, because the third lower row does not appear until somewhat later than the others. Thus the amount of extreme ratio is also infinite in each instance, and for this reason the ratio of any combination involving the third lower row would be of no value as a character constant throughout the larval period of this species, i.e., *Pseudacris nigrita triseriata*. Of course the absence of a given row for a given body size might be a valuable character. However, the discussion at this point does not deal with this aspect. Also, the maximum ratio in the restricted range in each instance in this group is taken as the case in which the third lower row is shortest, though present. This omits a much greater percentage of cases than in other combinations. For this reason, then, the combinations considered in this group cannot be "fairly" compared with other combinations. However, the combinations of this group may be evaluated with respect to each other.

Summary of the Combinations of Rows.—From a study of the results expressed in Table IX and subcolumns "A" of Table X it may be stated that the following is the order of the different possible combinations of rows of teeth from least to greatest variability of ratio and from greatest to least value as constant characters through the period of

TABLE IX.—*Pseudactis nigrita triseriata*: RATIOS TO ONE OF DIFFERENT COMBINATIONS OF MOUTHPARTS

Combinations	Extreme range			Restricted range			Variation %	Range in older animals			Relative Age of	
	Minimum	Maximum	Amount	Minimum	Maximum	Amount		Minimum	Maximum	Amount	Minimum	Maximum
1 U/2 U.....	1.00	1.25	0.25	1.02	1.18	0.16	7.3	1.00	1.18	0.18	O	vY
1 U/1 L.....	0.98	1.72	0.74	1.08	1.44	0.36	14.3	1.08	1.32	0.24	M	vY
1 U/2 L.....	1.00	1.96	0.96	1.03	1.37	0.34	14.2	1.03	1.28	0.25	M	vY-Y
1 U/3 L.....	2.94	inf.	inf.	3.20	22.33	19.13	74.1	2.94	5.60	2.66	vO	M
2 U/1 L.....	0.84	1.37	0.53	0.98	1.28	0.30	13.3	1.01	1.22	0.21	M	M
2 U/2 L.....	0.83	1.36	0.51	0.92	1.31	0.39	17.9	0.92	1.18	0.26	M	M
2 U/3 L.....	2.22	inf.	inf.	2.65	20.00	17.35	76.6	2.65	5.50	2.85	M	vY
1 L/2 L.....	0.82	1.20	0.38	0.87	1.08	0.21	10.8	0.87	1.01	0.14	vY	Y
1 L/3 L.....	2.31	inf.	inf.	2.68	17.00	14.32	72.8	2.31	7.00	4.69	vO	vY
2 L/3 L.....	2.54	inf.	inf.	2.76	18.00	15.24	73.4	2.54	4.72	2.18	vO	vY-Y
1 U/r & 1.....	2.20	5.01	2.81	2.32	3.60	1.28	21.6	2.32	3.05	0.73	M	Y
2 U/r & 1.....	1.89	3.51	1.62	2.04	3.21	1.17	22.4	1.89	3.51	1.62	M-O	M-O
1 L/r & 1.....	1.81	3.04	1.23	1.88	2.88	1.00	21.0	1.81	2.46	0.65	M-O	vY
2 L/r & 1.....	1.65	3.28	1.63	1.91	3.02	1.11	22.7	1.83	2.73	0.90	Y	Y-M
3 L/r & 1.....	inf.	0.92	inf.	0.14	0.80	0.66	70.0	0.42	0.84	0.42	vY	M
2 U/m s.....	1.70	9.60	7.90	2.32	6.50	4.18	45.0	2.32	9.60	7.28	vY	vO
r & 1/m s.....	0.48	4.28	2.80	0.82	2.86	2.04	55.4	1.00	4.28	3.28	vY	vO
1 U/M.....	1.45	2.50	1.05	1.55	2.16	0.61	16.7	1.70	2.16	0.46	Y	Y
2 U/M.....	1.36	2.68	1.32	1.43	1.93	0.50	14.9	1.54	2.00	0.40	vY	M
1 L/M.....	1.00	2.20	1.20	1.22	1.91	0.69	22.3	1.22	1.91	0.69	vY	vY
2 L/M.....	1.10	2.31	1.21	1.20	1.89	0.69	22.6	1.34	1.94	0.60	vY	M
3 L/M.....	inf.	0.64	inf.	0.07	0.59	0.52	44.1	0.34	0.64	0.30	vY	vO
r & 1/M.....	0.40	1.17	0.77	0.46	0.82	0.36	28.1	0.49	0.93	0.44	vY	M

Symbols used for rows, etc., are the same as in Table V. "M" is upper beak.

TABLE X.—*Pseudacris nigrita triseriata*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE IX

Combinations of rows, etc.	Criteria										Final assigned values	
	Amount of extreme range of ratios		Amount of restricted range of ratios		Percentage varia- tion of restricted range of ratios		Amount of range of ratios in older animals		Amount of dif- ference between range in older animals and re- stricted range			
									A	B		
	A*	B†	A	B	A	B	A	B	A	B	A	B
1 U/2 U.....	1	1	1	1	1	1	2	2	1	2	1	1
1 L/2 L.....	2	2	2	2	2	2	1	1	2	4	2	2
2 U/1 L.....	4	4	3	3	3	3	3	3	3-4	6-8	3	3
1 U/2 L.....	6	7	4	4	4	4	5	5	3-4	6-8	4	4
1 U/1 L.....	5	5	5	5-6	5	5	5	4	5	9	5	5
2 U/M.....	5	12	2	8	1	6	3-4	10-11	2	3	1	7
1 U/M.....	2	8	4	10	2	7	3-4	10-11	5	11	3	9
2 U/2 L.....	3	3	6	7	6	8	6	6	6	10	6	6
1 L/r & 1.....	7	11	8	14	7	9	8	13	9	15	7	12
1 U/r & 1.....	11	16	11	17	8	10	9	15	11	17	10	15
1 L/M.....	3	9	5-6	12-13	3	11	6	4	1	1	4	10
2 U/r & 1.....	8	13	10	16	9	12	11	17	10	16	9	14
2 L/M.....	4	10	5-6	12-13	4	13	5	12	4	16	...	11
2 L/r & 1.....	9	14	9	15	10	14	10	16	7	12	8	13
r & 1/M.....	1	6	1	5-6	5	15	2	9	3	5	2	8
3 L/M.....	6	?	3	9	6	16	1	7	6	13	5	18
2 U/m s.....	12	17	13	19	11	17	17	23	13	19	12	17
r & 1/m s.....	10	15	12	18	12	18	15	21	12	18	11	16
3 L/r & 1.....	?	?	7	11	13	19	7	8	8	14	13	19
1 L/3 L.....	?	?	14	20	14	20	16	22	14	20	15	21
2 L/3 L.....	?	?	15	21	15	21	12	18	15	21	14	20
1 U/3 L.....	?	?	17	23	16	22	13	19	17	23	17-16	23-22
2 U/3 L.....	?	?	16	22	17	23	14	20	16	22	16-17	22-23

*Sub-columns headed "A" give ranks of combinations within groups, which groups are (1) combinations involving only the rows of teeth, or (2) combinations involving the rows of teeth on the one hand and the upper beak on the other.

†Sub-columns headed "B" give ranks of combinations as compared with all other combinations.

Symbols used to represent rows are the same as in Table V. "M" is upper beak.

larval existence of *Pseudacris nigrita triseriata* covered by the present study: (1) first upper/second upper; (2) first lower/second lower; (3) second upper/first lower; (4) first upper/second lower; (5) first upper/first lower; (6) second upper/second lower; (7) first lower/average of right and left parts of second upper; (8) second lower/average of right and left parts of second upper; (9) Second upper/average of right and left parts of second upper; (10) first upper/average of right and left parts of second upper; (11) average of right and left parts of second upper/median space in second upper; (12) second upper/median space in second upper; (13) third lower/average of right and left parts of second upper; (14) second lower/third lower; (15) first lower/third lower; (16)-(17) second upper/third lower; (16)-(17) first upper/third lower.

Combinations Involving the Upper Beak.—Subcolumns "A" in Table X show the rank of each combination involving the upper beak according to the same criteria used in evaluating combinations involving only the rows of teeth (cf. also Chart 7).

All ranges of ratios of all combinations of rows of teeth with upper beak are quite similar except in those combinations involving (1) the average of the right and left parts of the second upper row, and (2) the third lower row. Of these two combinations the latter must be counted as least in value because of the late appearance of the third lower row. The former of these two combinations may be considered as ranking first least when all criteria are considered.

The other four combinations, i.e., those involving the first upper, second upper, first lower, and second lower rows respectively do not differ considerably from each other according to any criterion. However, when all criteria are considered, the ratios of the combinations involving the four rows in question rank from least to greatest as follows: second upper, first upper, first lower, and second lower respectively.

Thus, the rank of the different respective combinations involving the upper beak from least to greatest range and variability of ratio and from greatest to least value as a constant character is as follows: (1) average of right and left parts of the second upper row/upper beak; (2) second upper row/upper beak; (3) first upper row/upper beak; (4) first lower row/upper beak; (5) second lower row/upper beak; and (6) third lower row/upper beak.

As a group these combinations are of a rank of value somewhat higher as affording ratios as constant characters than the group of combinations involving the averages of right and left parts of the second upper row, and perhaps slightly less than the group of combinations involving only the four longer rows. Individual combinations, of course, will vary some-

what from such an exact rank. For instance, the combination, third lower row/upper beak, will rank along with the other combinations involving the third lower row.

Comparative Evaluation of All Combinations.—If all combinations, both those involving only the rows of teeth or their parts, and those involving rows of teeth or their parts and the upper beak, be considered collectively according to all criteria, they will be found to rank as follows from greatest to least value as constant characters of the tadpoles of *Pseudacris nigrita triseriata* (cf. subcolumns "B" in Table X): (1) first upper row/second upper row; (2) first lower row/second lower row; (3) second upper row/first lower row; (4) first upper row/second lower row; (5) first upper row/first lower row; (6) second upper row/second lower row; (7) second upper row/upper beak; (8) average of right and left parts of second upper row/upper beak; (9) first upper row/upper beak; (10) first lower row/upper beak; (11) second lower row/upper beak; (12) first lower row/average of right and left parts of second upper row; (13) second lower row/average of right and left parts of second upper row; (14) second upper row/average of right and left parts of second upper row; (15) first upper row/average of right and left parts of second upper row; (16) average of right and left parts of second upper row/median space in second upper row; (17) second upper row/median space in second upper row; (18) third lower row/upper beak; (19) third lower row/average right and left parts of second upper row; (20) second lower row/third lower row; (21) first lower row/third lower row; (22) second upper row/third lower row; (23) first upper row/third lower row.

Rana pipiens

DESCRIPTIONS OF THE PARTS OF THE MOUTH APPARATUS

The number and disposition of the rows of teeth, when all are present, in *Rana pipiens* are the same as the common type described in the introduction (cf. pp. 9-11).

After the upper beak is heavily pigmented or has begun to be apparent, teeth of the first upper row and first lower row appear, followed shortly by the appearance of teeth in the second and third lower rows. The second upper row is quite irregular as to appearance and occurrence.

There is a great degree of irregularity in the animals studied in this series (one hundred individuals, of body lengths from 4.15 mm. to 8.47 mm.).

In the first upper row there occur obvious irregularities in 15% of the animals studied.

The second upper row is entirely absent in 66% of the cases studied. In an additional 5% the row is either very faint or only one of its parts is present. At any rate in only 29% of the cases could satisfactory measurements and counts be taken. (For further discussion cf. below.)

The first lower row is relatively complete and regular in only 28% of the cases studied.

The second lower row is entirely absent when other rows are present in 6% of the cases. It is irregularly divided in other than the median line in 7% of the cases studied.

Although the third lower row shows no tendency to divide into two equal parts, in 8% of the cases it is divided irregularly into from two to an indefinite number of parts. This 8% does not include the many cases in which the teeth in a row are themselves scattered and irregularly distributed. The row is absent in 8% of the cases, and consists of one (visible) tooth in an additional 2%.

The irregularities through the series of *Rana pipiens* studied show practically no correlation with body size or age. The second upper row in a very general way appears with increase in body size (length). The body lengths in the series range from 4.15 mm. to 8.47 mm.; and the smallest animal having the second upper row is 4.65 mm. in body length, while the largest animal not having a second upper row is 7.30 mm. in body length. No other irregularities show even this degree of correlation.

CURVATURE OF THE ROWS OF TEETH

Table XI gives the ratios of arc length/chord length for the rows of teeth of this species, i.e., *Rana pipiens*. The series of tadpoles of this species studied did not attain as great a proportionate size of the species as was the case in the series of the other two species studied. Therefore, from the viewpoint of proportion of possible size attained, the tadpoles

TABLE XI.—*Rana pipiens*: RATIOS TO ONE OF ARC LENGTH/CHORD LENGTH OF ROWS OF TEETH

Row	Maximum (all included)	Maximum (less extremes)	Minimum
First upper.....	1.35	1.18	1.04
Right part of second upper...	1.12	1.12	1.00
Left part of second upper.....	1.25	1.10	1.00
First lower.....	1.26	1.16	1.03
Second lower.....	1.32	1.27-1.18	1.01
Third lower.....	1.30	1.12	1.00

of *Rana pipiens* studied should be compared only with the smaller tadpoles of *Bufo fowleri* and of *Pseudacris nigrita triseriata*.

However, in general practically as great arc length/chord length ratios develop in *R. pipiens* as in the other species (cf. Tables XI, VII, and II.) Now in actual range of body size the tadpoles of the series of the different species studied do not differ greatly. Therefore, it may be concluded that arc length/chord length ratios of the rows of teeth correspond more to actual body size than to proportion of possible body size.

There is in *Rana pipiens* a general tendency for an increased arc length/chord length ratio in more peripheral rows of teeth.

NUMBERS OF TEETH IN THE DIFFERENT ROWS OF TEETH

There is no apparent change with age of numbers of teeth per unit arc length of the rows of teeth in the tadpoles of the series of *Rana pipiens* studied. The size attained by the tadpoles of the series is, however, small as compared with possible size; and perhaps no such change could be expected without much larger animals being studied.

Minimum numbers of teeth per unit arc length of row are slightly less than in *Bufo fowleri* and much less than in *Pseudacris nigrita triseriata*. Maximum numbers of teeth per unit arc length of row are much less than in *B. fowleri* and very much less than in *P. nigrita triseriata* (cf. Tables XII, VIII, and III). The differences between maximum and minimum numbers of teeth per unit arc length of row ("range" in the Tables) are also somewhat less in *R. pipiens* than in the other species. This fact may, however, be due to the elimination from consideration of so many rows of teeth, i.e., rows irregularly or only partly toothed. It may be noted, however, that, since numbers of teeth per unit arc length of row are in general less in *R. pipiens* than in the other species studied, it follows that the teeth are generally larger in the tadpoles of *R. pipiens* than in tadpoles of the other two species.

TABLE XII.—*Rana pipiens*: NUMBER OF TEETH PER 1 MM. OF ARC LENGTH OF ROW OF TEETH

Row	Maximum	Minimum	Range
First upper.....	53	31	22
Right part of second upper...	58	27	31
Left part of second upper....	67	28	39
First lower.....	60	38	22
Second lower.....	62	32	30
Third lower.....	59	28	31

TABLE XIII.—*Rana pipiens*: RATIOS TO ONE OF THE DIFFERENT COMBINATIONS OF MOUTH PARTS

Combinations of rows, etc.	Extreme range			Restricted range			% variation	Range in older animals			Relative age of	
	Mini- mum	Maxi- mum	Amount	Mini- mum	Maxi- mum	Amount		Mini- mum	Maxi- mum	Amount	Mini- mum	Maxi- mum
1 U/2 U.....	1.05	inf.	inf.	1.05	1.56	0.51	29.0	O	O
1 U/1 L.....	zero	inf.	inf.	1.05	2.19	1.14	35.2	1.12	2.32	1.20	Y	M
1 U/2 L.....	zero	inf.	inf.	0.90	2.47	1.49	43.4	1.12	1.87	0.75	Y	Y
1 U/3 L.....	zero	inf.	inf.	1.53	14.20	12.67	80.6	1.52	12.65	11.13	Y	Y
2 U/1 L.....	zero	inf.	inf.	0.81	3.16	2.35	59.3	O	O
2 U/2 L.....	zero	inf.	inf.	0.74	2.32	1.58	51.6	M	O
2 U/3 L.....	zero	inf.	inf.	0.89	14.33	13.44	88.3	Y	M
1 L/2 L.....	0.08	inf.	inf.	0.78	10.00	9.22	85.5	M	Y&M
1 L/3 L.....	0.07	inf.	inf.	0.88	8.60	7.72	81.2	1.13	1.86	0.73	M	Y&M
2 L/3 L.....	0.62	inf.	inf.	1.03	8.20	7.17	77.7	1.08	1.62	0.54	M	Y-M
1 U/r & 1.....	3.02	inf.	inf.	3.77	21.50	17.73	70.2	O	O
2 U/r & 1.....	3.25	20.00	16.75	3.52	15.75	12.23	63.6	all	all
1 L/r & 1.....	zero*	inf.	inf.	1.38	24.33	22.95	89.3
2 L/r & 1.....	zero†	inf.	inf.	1.53	27.00	25.47	89.3
3 L/r & 1.....	0.69	inf.	inf.	1.38	18.00	17.19	91.4
2 U/m s.....	1.03	inf.	inf.	0.81	2.22	1.12	34.0
r & 1/m s.....	1.42	17.67	16.25	1.10	6.33	6.26	97.8	all	all
1 U/M.....	0.96	1.60	0.64	1.05	1.52	0.47	19.0	1.22	1.60	0.38	M	O
2 U/M.....	zero	inf.	inf.	0.84	1.32	0.48	22.2	M	O
1 L/M.....	inf.	1.33	inf.	0.34	1.19	0.85	55.8	all	M
2 L/M.....	inf.	1.30	inf.	0.50	1.24	0.74	42.5	inf.	1.26	inf.	all	M&O
3 L/M.....	inf.	1.10	inf.	0.10	0.90	0.80	80.0	inf.	1.27	inf.	all	O
r & 1/M.....	inf.	0.48	inf.	0.06	0.38	0.32	72.7	all	Y

Note: Symbols for rows used in this table are the same as in Table V. Inf. = Infinitly.

*When r&l = zero, 1 L may be 0.21 to 0.96 mm.; when 1 L = zero, r&l may be 0.15 to 0.30 mm.

†When r&l = zero, 2 L may be 0.20 to 0.90 mm.; when 2 L = zero, r&l may be 0.15 mm.

‡When r&l = zero, 3 L may be 0.05 to 0.63 mm.

*"M" is upper beak.

RATIOS OF COMBINATIONS OF ROWS OF TEETH AND OF ROWS
OF TEETH AND UPPER BEAK

Because of such irregularity and of the frequent absence of entire rows, ratios are quite likely to be very irregular and have rather wide ranges in *R. pipiens*. The extreme range of ratio of any combination (except combinations involving only the parts of a single row) is, due to the frequent absence of individual rows, in every instance infinite. The restricted range, as given in Table XIII, includes all cases in which both rows of the combination in question are present if in as many as or more than 5-6% of the cases one of the rows is absent. If in less than 5-6% of the cases one of the rows is absent, the restricted range omits a sufficient number of exceptional cases where both rows are present to make up the 5-6%. Too, the range of sizes of the tadpoles of this series is so small as compared with the size attained before metamorphosis that the range of ratio in "older" animals is without much significance other than indicating the "trend" of the ratios. Too few animals possess the second upper row to segregate the animals as to age in the cases of combinations involving this row or its parts.

Combinations Not Involving the Second Upper Row.—The rank according to value of constancy of ratio of the combinations in this group is as follows: (1) first upper row/first lower row, (2) first upper row/second lower row, (3) second lower row/third lower row, (4) first lower row/third lower row, (5) first lower row/second lower row, and (6) first upper row/third lower row.

Combinations Involving the Second Upper Row and Its Parts.—Since the combinations in this group involve less than one-third of the animals studied, the group is too small to divide with respect to age. Thus, the only criteria to be used in evaluating the combinations are amount of restricted range of ratio and percentage variation of this range.

The following combinations of this group rank in the order listed from least to greatest according to either or both of the above mentioned criteria: (1) first upper row/second upper row, (2) second upper row/median space of second upper row, (3) second upper row/second lower row, and (4) second upper row/first lower row.

In the remaining combinations of this group relative amounts and percentages differ. Considering both criteria, however, the combinations rank from least as follows: (5) second upper row/average of right and left parts of second upper row, (6) second upper row/third lower row, (7) first upper row/average of right and left parts of second upper row, (8) average of right and left parts of second upper row/median space in second upper row, (9) third lower row/average of right and left parts

TABLE XIV.—*Rana pipiens*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE XIII

Combinations of rows, etc.		Criteria									Final assigned relative values		
		Amount of restricted range of ratio			Percentage variation of restricted range of ratio			Per both the preceding criteria					
								A	B	C			
Set	Group	A*	B*	C*	A	B	C	A	B	C	A	B	C
		9	3	1	5	3	1	6-7	3	1	2	2	1
		10	4	2	7	4	2	9	4	2	5	2	2
		14	8	3	14	9	3	13-15	7-9	3	7	3	3
		15	9	4	17	11	5	16	10	4	8	4	4
	Group	17	11	5	18	12	6	13-15	7-9	5	10	6	6
		10	12	6	16	10	4	18	12	6	9	5	5
		1 U/2 U.....	4	1	1	2	1	2-3	1	1	12	7	1
		2 U/m s.....	8	2	2	4	2	5	2	2	13	8	2
		2 U/2 L.....	11	5	3	8	5	3	10	5	15	9	3
Group	12	6	4	10	6	4	13-15	7-9	4	16	10	4	
	13	7	5	23	17	11	19	13	8	20	14	8	
	16	10	6	11	7	5	12	6	5	17	11	5	
	2 U/r & 1.....	19	13	7	19	13	7	20	14	18	12	6	
	3 L/r & 1.....	20	14	8	22	16	10	21	15	21	15	9	
Group	21	15	9	12	8	6	17	11	7	19	13	7	
	1 U/r & 1.....	22	16	10	20-21	14-15	8-9	22	16	22	16	10	
	1 L/r & 1.....	23	17	11	20-21	14-15	8-9	23	17	23	17	11	
	2 L/r & 1.....												
Set	Group	2 U/M.....	2	1	1	1	1	1	1	1	1	1	1
		1 L/M.....	7	4	4	9	4	3	8	5	4	3	3
		2 L/M.....	5	6	2	6	3	2	4	3	3	2	2
		3 L/M.....	6	5	3	15	7	4	11	6	3-4	6	4
Set	Group	2 U/M.....	3	2	3	2	1	2-3	2	1	11	5	1
		r & 1/M.....	1	1	1	13	5	2	6-7	4	2	14	6

*Sub-columns headed "A" give relative values of the combinations when all are considered; sub-column "B" the relative values within a "set," and sub-column "C" the relative values within a "group."

Symbols used for rows are the same as in Table V. "M" is upper beak.

of second upper row, (10) first lower row/average of right and left parts of second upper row, and (11) second lower row/average of right and left parts of second upper row.

Combinations Involving the Upper Beak.—The combinations in this group rank from greatest to least value of constancy as follows (cf. subcolumns "B" and "C" in Table XIV, and Chart 8): (1) first upper row/upper beak, (2) second lower row/upper beak, (3) first lower row/upper beak, (4) third lower row/upper beak, (5) second upper row/upper beak, (6) average of right and left parts of second upper row/upper beak.

Summary.—The relative values within the groups of the various combinations as affording ratios of reliable constancy in the series studied of this species, *Rana pipiens*, have been given and will not be repeated here. However, the relative values of all combinations, (not grouped) according to all criteria and taking into account the high percentage of absence of the second upper row, may be listed as follows from greatest to least value (cf. subcolumns "A" in Table XIV): (1) first upper row/upper beak; (2) first upper row/first lower row; (3) second lower row/upper beak; (4) first lower row/upper beak; (5) first upper row/second lower row; (6) third lower row/upper beak; (7) second lower row/third lower row; (8) first lower row/third lower row; (9) first upper row/third lower row; (10) first lower row/second lower row; (11) second upper row/upper beak; (12) first upper row/second upper row; (13) second upper row/median space in second upper row; (14) average of right and left parts of second upper row/upper beak; (15) second upper row/second lower row; (16) second upper row/first lower row; (17) second upper row/average of right and left parts of second upper row; (18) second upper row/third lower row; (19) first upper row/average of right and left parts of second upper row; (20) average of right and left parts of second upper row/median space in second upper row; (21) third lower row/average of right and left parts of second upper row; (22) first lower row/average of right and left parts of second upper row; and (23) second lower row/average of right and left parts of second upper row.

It will be noted that the relative values of the combinations in *Rana pipiens* do not correspond to a very great extent to the relative values of similar combinations in *P. nigrata triseriata* or in *Bufo fowleri*. If the relative values of the combinations (in *R. pipiens*) be estimated without taking into consideration the high percentage of absence of the second upper row (cf. Table XV) the values correspond to a greater extent, but even by this method of comparison the extent to which the different species correspond is not great. This will be further discussed below.

*General Considerations Involving All Species Studied*COMPARISON OF EVALUATIONS OF RATIOS
IN THE DIFFERENT SPECIES

Through examination of Table XV it will be seen that the corresponding combinations of rows of teeth and of rows of teeth and upper beak do not have the same relative rank (according to value as affording constant characters) in the different species studied, i.e., *B. fowleri*, *P. nigrita triseriata*, and *R. pipiens*. The greater similarity in relative values of corresponding combinations is between *B. fowleri* and *P. nigrita triseriata*. *R. pipiens* is quite different from either *B. fowleri* or *P. nigrita triseriata* in relative values of constancy of ratios of corresponding combinations.

It has been seen that the third lower row appears rather late in *P. nigrita triseriata*, thus making the combinations involving this third lower row of less value than any other combinations. Now, if combinations involving this third lower row be eliminated in both *B. fowleri* and *P. nigrita triseriata* and the remaining combinations have their relative values redetermined on the basis of the reduced number, then the relative values of corresponding combinations in the two species, *B. fowleri* and *P. nigrita triseriata* will coincide to a much greater degree. Of the seventeen combinations thus compared there is exact coincidence of rank in six cases, a difference in rank of one in six cases, a difference of two in

TABLE XV.—NUMERICAL RANK FROM GREATEST TO LEAST VALUE FOR CONSTANCY OF RATIO OF DIFFERENT COMBINATIONS OF MOUTH PARTS COMPARED IN SPECIES STUDIED

Combination of rows, etc.	Order of relative value			Combination of rows, etc.	Order of relative value		
	<i>B. fowleri</i>	<i>P. nigrita triseriata</i>	<i>R. pipiens</i>		<i>B. fowleri</i>	<i>P. nigrita triseriata</i>	<i>R. pipiens</i>
1 U/2 U.....	1	1	12	1 U/3 L...	13	23	9
1 L/2 L.....	2	2	10	2 L/3 L...	14	20	7
2 U/1 L.....	3	3	16	3 L/r & 1...	15	19	21
2 U/2 L.....	4	6	15	2 U/r & 1...	16	14	17
1 U/2 L.....	5	4	5	2 U/3 L...	17	22	18
1 U/1 L.....	6	5	2	1 L/r & 1...	18	12	22
1 U/M.....	7	9	1	1 U/r & 1...	19	15	19
2 U/M.....	8	7	11	2 L/r & 1...	20	13	23
1 L/M.....	9	10	4	r & 1/M...	21	8	14
2 L/M.....	10	11	3	r & 1/m s...	22	16	20
3 L/M.....	11	18	6	2 U/m s...	23	17	13
1 L/3 L.....	12	21	8				

Symbols for rows of teeth are the same as in Table V.

three cases, a difference of three in one case, and in one case a difference of seven. It appears that this is a rather high degree of correlation.

In *R. pipiens* the second upper row has been noted to be absent in almost two-thirds of the animals studied. Thirteen of the twenty-three possible combinations involve this second upper row or its parts or median space. If *R. pipiens* and *B. fowleri* be compared as to respective relative values of the ten combinations not involving the second upper row in any way, the extent of correlation is indeed not great. There is exact coincidence of rank in only two cases; a difference of one in three cases, a difference of three in four cases, and a difference of nine in one case.

If *P. nigrata triseriata* and *R. pipiens* be compared as to relative values of the only six combinations not involving either the third lower row or the second upper row in any way, practically no correlation exists. There is no coincidence of rank, a difference of one in rank in two cases, a difference of three in three cases, and a difference of five in one case. It is true, however, that the six combinations used in this comparison are of not so different actual values in any species studied, and of uncertain relative rank in some instances.

Thus, according to relative rank of corresponding combinations (involving only regular rows), *B. fowleri* and *P. nigrata triseriata* correspond more nearly than any other two species; and *B. fowleri* and *R. pipiens* correspond more nearly than *P. nigrata triseriata* and *R. pipiens*. The "fairness" of such comparisons may be debated. It might appear that comparison on the basis of such a small number of combinations is not sufficiently likely to show much correlation of rank. However, it must be kept in mind that it is granting a point to eliminate from the comparisons the constant "irregularities." Hence, the comparisons as made above show greater degrees of correlation than actually exist. For the constantly high percentage of absence of a given row cannot be overlooked.

It appears, then, that if "irregularities" be overlooked, growth phenomena in the different species may be quite similar. This may actually be true of growth phenomena of the oral disc in general; and the general conclusions as to growth phenomena as drawn from the analyses of the series of *B. fowleri* tadpoles may be concluded to apply to the other species studied. However, the general conclusions do not apply to specific rows, and hence to combinations of rows. Each species constitutes an individual case; and, though the same general phenomena may underlie all cases, each species must have its own combinations of rows and of rows and upper beak relatively evaluated strictly on their own merits of constancy.

RESULTS OF PRESENT STUDY COMPARED WITH CHARACTERS
USED BY WRIGHT

Since one of the first objectives in beginning the present study was to determine to what extent, if any, the characters used by Wright as applying to "mature" tadpoles apply to young tadpoles, a comparison may now be made between the characters used by Wright and the results of the present study.

Bufo fowleri.—Wright (1929) describes and places in the "key" the tadpole of a toad to which he refers as "Bufo (Raleigh)." In the "key" included in the *Frogs of the Okefinokee* (1932), the section giving a synopsis of the "Bufo (Raleigh)" tadpoles is used without change to describe the tadpoles of *Bufo fowleri*. It is to be concluded from this that the characters of *B. fowleri* tadpoles are rather constant throughout the geographical range of the species, for Wright has undoubtedly examined tadpoles of this species from a variety of localities. Now, if what Wright means by "normally" corresponds in a general way to "restricted range of ratios" of the author, characters used by Wright should practically coincide with those determined by the author if the characters used by Wright are of any value when applied to all sizes of tadpoles. This should be especially true for *B. fowleri*, since the present study involves tadpoles of maximum size. Examination of Table XVI will reveal that the ranges of ratios of the combinations used as given by Wright are considerably less than those obtained in the present study (no exceptions). In only two instances does the range as given by Wright fail to fall completely within the range determined by the present study. Also, the ranges for *B. americanus* and *B. terrestris* fall within the respective ranges of *B. fowleri* as determined by the present study.

TABLE XVI.—RATIOS OF *Bufo fowleri* COMPARED WITH RATIOS GIVEN BY WRIGHT
FOR SPECIES OF *Bufo*

Combinations of rows, etc.	Ratios given by Wright (1929)			Ratios obtained in present study
	<i>B. terrestris</i>	<i>B. fowleri</i>	<i>B. americanus</i>	
1 U/M.....	1.75	1.4-1.5	1.2-1.4	1.48-1.94
1 L/M.....	1.5	1.2-1.3	1.1-1.2	1.17-1.62
2 L/M.....	1.5	1.2-1.3	1.1-1.2	1.10-1.56
1 L/3 L.....	1.2-1.4	1.3-1.6	1.3-1.5	1.05-1.85
r & 1/m s.....	1.4-2.1	1.3-3.0	1.15-2.0	0.60-2.64
3 L/M.....	1.0 or slightly more	1.0-	0.80-1.33
1 U/2 U.....	1.0 or greater	0.98-1.22

Symbols used for rows of teeth, etc., are the same as in Table V.

Furthermore, if the ratios of the older animals of the series studied be examined, it will be seen that such ratios fall without exception in the upper values of the respective ranges as given in the present study, and, hence, for the most part, are above the maximum ranges given by Wright. Thus, two conclusions are obvious. (1) The range of ratios of any given combination as given by Wright for mature tadpoles of *B. fowleri* is not of sufficient extent to apply to younger tadpoles. (2) The range of ratios of any given combination as given by Wright is too narrow to include a "normal" percentage of mature tadpoles of *B. fowleri* over the geographical range of the species.

Now if the "normal" range of ratio of a given combination in a given species be of sufficient extent to apply to the cases of younger, as well as mature tadpoles, will the ratio in question be of any value as a distinctive character? This question will be further discussed later.

Pseudacris nigrita triseriata.—Wright (1929) described "Pseudacris (Buffalo)," "Pseudacris (Raleigh)," and *P. ocularis*, and in *Frogs of the Okefinokee* (1932) discussed to some extent also *P. nigrita*. The Pseudacris from Buffalo lacks the third lower row of teeth, although tadpoles described have "embryonic hind legs" and a maximum body length of 8.8 mm. Further, the tadpoles are spoken of as being "quite small." Even though the largest tadpoles of the series examined in the present study are not so large as the "quite small" Pseudacris from Buffalo, the fact that the third lower row of teeth appears later than the other rows in the tadpoles of this series of *Pseudacris nigrita triseriata* raises several questions. If the "Pseudacris (Buffalo)" is a different species, perhaps there may be some systematic significance attached to the order or time of appearance of the rows of teeth. This is, however, unlikely. Or the late appearance of the row in question or its failure to appear may also be a geographical variation. Would the third lower row have appeared later in the "Pseudacris (Buffalo)"? Or had it been lost? Wright apparently presumes its absence to be a specific character. In fact a rather confusing state of affairs prevails, since in the Wrights' *Handbook of Frogs and Toads* (1933) the tadpoles of *Pseudacris nigrita triseriata* are described as having two upper and two lower rows of teeth: ". . . and the tooth ridges 2/2" (line 13, page 95). This is obviously erroneous, unless a geographical variation in the numbers of rows of teeth occurs in the species.

In the series examined in the present study, tadpoles as small as 2.91 mm. (body length) may have a distinct third lower row; and the row is never absent in tadpoles of more than 3.36 mm. body length, though the teeth may be barely pigmented sufficiently to be readily detected when the tadpoles are as large as 3.57 mm. body length. It appears, then, that the

tadpoles upon which Wright and Wright (1933) base the description of *P. nigrita triseriata* tadpoles may not be *P. nigrita triseriata* tadpoles at all.

Table XVII gives the ranges of ratios used by Wright (1929) in describing tadpoles of "Pseudacris (Raleigh)" and *P. ocularis* as compared with the ranges of the corresponding ratios in the tadpoles of *P. nigrita triseriata* examined in the present study. Wright does not describe *P. nigrita* tadpoles in *Frogs of the Okefinokee* (1932), although he discusses at length the life history of the species. Neither are ratios of combinations of rows given by Wright and Wright (1933).

TABLE XVII.—RATIOS OF *Pseudacris nigrita triseriata* COMPARED WITH RATIOS GIVEN BY WRIGHT FOR SPECIES OF *Pseudacris*

Combinations of rows, etc.	Ratios given by Wright (1929)		Ratios obtained in present study
	<i>P. (Raleigh)</i>	<i>P. ocularis</i>	<i>P. nigrita triseriata</i>
1 U/M.....	1.50-1.75	2.0	1.55-2.16
1 L/M.....	1.25-1.60	2.0	1.22-1.91
2 L/M.....	1.25-1.60	2.0	1.20-1.89
1 L/3 L.....	3.00-4.00	3.0	2.68-17.00
r & 1/m s.....	2.50-7.00	3.0-4.0	0.82- 2.86

Symbols used for rows of teeth, etc., are the same as in Table V.

The ranges of ratios as determined in the present study of *P. nigrita triseriata* include the respective ranges of ratios of Wright's "Pseudacris (Raleigh)" with one exception, and on the basis of this one ratio (average of right and left parts of second upper row/median space in same) the two species may be separated, provided the range Wright assigns includes actually a "normal" percentage of the tadpoles of the species. *P. ocularis* tadpoles may be distinguished from *P. nigrita* tadpoles by three ratios, provided the ratios as given by Wright for *P. ocularis* are as "exact" or limited as they are listed, which they perhaps are not.

Unfortunately, there is no detailed description of the mouthparts of mature *P. nigrita triseriata* tadpoles with which the present findings may be compared; and the reliability of applying the ratios obtained in this study to "mature" tadpoles must await examination of a series including larger tadpoles before being determined.

Rana pipiens.—The ratios of combinations of rows of teeth, etc., of the tadpoles of the series of this species examined in the present study may be compared with the ratios given by Wright for this species and

for *R. sphenoccephala*, *R. palustris*, and *R. clamitans* by examination of Table XVIII. In the case of the ratio of each combination the range established by the present study will include the ranges for all the species compared. It appears, then, that the ranges of ratios as given by Wright for *R. pipiens* must be considerably extended in order to be applicable to young tadpoles, with the result that the ratios of the combinations of rows he uses lose their distinction.

TABLE XVIII.—RATIOS OF *Rana pipiens* COMPARED WITH RATIOS GIVEN BY WRIGHT FOR SPECIES OF *Rana*

Combinations of rows, etc.	Ratios given by Wright (1929)				Ratios obtained in present study
	<i>R. clamitans</i>	<i>R. palustris</i>	<i>R. sphenoccephala</i>	<i>R. pipiens</i>	<i>R. pipiens</i>
1 U/M.....	1.0 (about)	1.0	1.0 or 1.0	1.0 or 1.0 (never 1.5)	1.05-1.52
1 L/M.....	1.0
2 L/M.....
1 L/3 L.....	2.0	1.49-3.03	1.4-1.49	1.28	0.88-8.60
r & 1/m s.....	0.09-0.17	0.25-0.50	1.0-2.00	0.67-1.00	0.07-6.33
3 L/M.....	0.75-0.80
1 U/2 U.....	?	1.0 or 1.0	"about" 1.0	1.05-1.56

Symbols used for rows of teeth, etc., are the same as in Table V.

Summary.—From the above comparisons it is first to be concluded that the ratios of combinations of rows as given by Wright for mature tadpoles are not of sufficiently extensive range to be applicable to younger tadpoles, nor, indeed, to be in some instances applicable to all "geographic races" of mature tadpoles of the species in question. And, further, when the ranges are extended to include the cases of younger tadpoles, there is the likelihood of the ratios used by Wright becoming of no specific distinctive value. This might indicate that perhaps ratios between rows of teeth are of little taxonomic value; but such a conclusion will not be drawn at this point for this particular aspect of the question will be further discussed later.

In particular, the tadpoles of *P. nigrita triseriata* examined in this series invariably have the third lower row of teeth after reaching a body length of 3.36 mm., although Wright and Wright (1933) describe the tadpoles of this species as having only two lower rows of teeth and do not mention the possibility of a third lower row being added. Either their identification or description is erroneous or there is a geographical difference in the tadpoles of the species.

COMPARISON OF THE DIFFERENT SPECIES STUDIED ACCORDING
TO RATIOS OF COMBINATIONS OF ROWS

If the three species of tadpoles studied, i.e., *B. fowleri*, *P. nigrita triseriata*, and *R. pipiens*, be compared as to restricted ranges of ratios of combinations of rows of teeth or of rows of teeth and upper beak, the more specifically distinctive ratios insofar as the species named are concerned may be determined. In Table XIX are listed the ratios of each combination for the different species; and the ratios may be readily compared by reference to this table. Examination of the table will also readily show which combinations afford ratios that are absolutely distinctive between any two given species of the three species studied.

In the cases of some combinations the ranges of the ratios overlap to a very great extent in the three species studied. However, these ratios are not to be considered as being of no distinctive value because of this overlapping of ranges. If two species cannot be distinguished on the basis of any single ratio, they possibly may be distinguished on the basis of several. Also, although the ranges of the ratios overlap, it is possible

TABLE XIX.—COMPARISON OF SPECIES STUDIED ACCORDING TO CRITERIA ESTABLISHED

Combinations of rows, etc.	Restricted range of ratios			Species* between which the ratio in question affords absolute distinction
	<i>B. fowleri</i>	<i>P. nigrita triseriata</i>	<i>R. pipiens</i>	
1 U/2 U.....	0.98-1.22	1.02- 1.18	1.05- 1.56
1 U/1 L.....	1.00-1.50	1.08- 1.44	1.05- 2.19
1 U/2 L.....	1.06-1.52	1.03- 1.37	0.98- 2.47
2 U/1 L.....	1.00-1.35	0.98- 1.28	0.81- 3.16
2 U/2 L.....	1.03-1.43	0.92- 1.31	0.74- 2.32
1 L/2 L.....	0.88-1.22	0.87- 1.08	0.78-10.00
1 U/3 L.....	1.30-1.22	3.20-22.33	1.53-14.20	Bf-Pnt
2 U/3 L.....	1.25-2.18	2.65-20.00	0.89-14.33	Bf-Pnt
1 L/3 L.....	1.08-1.85	2.68-17.00	0.88- 8.60	Bf-Pnt
2 L/3 L.....	1.06-1.86	2.76-18.00	1.03- 8.20	Bf-Pnt
1 U/r & 1.....	2.18-4.20	2.32- 3.60	3.77-21.50	Pnt-Rp
2 U/r & 1.....	2.13-3.46	2.04- 3.21	3.52-15.75	Rp-Pnt, Rp-Bf
1 L/r & 1.....	1.79-3.24	1.88- 2.88	1.38-24.33
2 L/r & 1.....	1.70-3.56	1.91- 3.02	1.53-27.00
3 L/r & 1.....	1.21-2.18	0.14- 0.80	0.81-18.00	Pnt-Bf, Pnt-Rp
2 U/m s.....	1.98-5.75	2.32- 6.50	1.10- 1.22	Pnt-Rp, Bf-Rp
r & 1/m s.....	0.60-2.64	0.82- 2.86	0.07- 6.33
1 U/M.....	1.48-1.94	1.55- 2.16	1.05- 1.52	Pnt-Rp, almost Bf-Rp
2 U/M.....	1.35-1.80	1.43- 1.93	0.84- 1.32	Pnt-Rp, Bf-Rp
1 L/M.....	1.17-1.62	1.22- 1.91	0.34- 1.19	Pnt-Rp, almost Bf-Rp
2 L/M.....	1.10-1.56	1.20- 1.89	0.50- 1.24	almost Pnt-Rp
3 L/M.....	0.80-1.33	0.07- 0.59	0.10- 0.90	Bf-Pnt, almost Bf-Rp
r & 1/M.....	0.50-0.79	0.46- 0.82	0.06- 0.38	Rp-Bf, Rp-Pnt

Symbols used for rows of teeth, etc., are the same as in Table X.

*Bf = *Bufo fowleri*; Pnt = *Pseudacris nigrita triseriata*; Rp = *Rana pipiens*.

to distinguish between species if the ratio of the combination in question happens to fall in any particular instance in that part of the range not duplicated. If, for instance, the combination, first upper row/second upper row, be considered, it may be seen that a ratio of less than 1.02:1.00 would, among the three species here considered, identify the tadpole in question as being *B. fowleri*. If the ratio were 1.02-1.04:1.00, the animal could not be *R. pipiens*. If the ratio were 1.05-1.17:1.00, the animal might be either of the three species. If the ratio were 1.18-1.22:1.00, the animal could not be *P. nigrita triseriata*, and if the ratio were greater than 1.22:1.00, the animal could only be *R. pipiens*. Thus, although the range of this ratio for all three species combined is only from 0.98:1.00 to 1.56:1.00, an "amount of range" of 0.58; this range is overlapped by all three species only from 1.05:1.00 through 1.18:1.00, or an "amount" of the range of 0.14, or about one-fourth of the total amount of range. Now, since the ranges as given in Table XIX are "restricted" ranges and hence include at least 94% of all cases, and since what ranges of ratios are given by Wright for the species involved in the present study are for the most part well within the ranges established by this study, it is safe to assume the ranges in Table XIX as quite reliable and quite apt to include all but exceptional cases (except where some row appears late, which would of itself be a character). Therefore, the ranges as here given are reliable to their limits; and should a ratio fall in the portion of a combined range of several species not overlapped by one or more species, this situation would constitute a valid reason for eliminating the possibility of the animal with such a ratio belonging to such "one or more" species.

Many cases, taken at random, may be properly classified on the basis of a single such ratio that is not absolutely distinctive, and a much greater percentage of cases may be properly classified on the basis of all such ratios. Further, although the ratios of such combinations are not individually nor indeed in the majority of cases distinctive when all are considered, some of them (e.g. ratios of combinations between the four longer rows of teeth) have been shown to be the most nearly constant of ratios of any and all combinations, and are, therefore, most reliable when they do happen to be distinctive.

GENERAL EVALUATION OF THE RATIOS OF THE COMBINATIONS OF ROWS

As to the various ratios afforded by all the various combinations of rows and of rows and upper beak, it may be concluded that each is of some value as a distinguishing character. The ratios that are less distinctive compensate by being more nearly constant in each species. The

actual combinations affording the ratios of more distinctive character are (1) those involving on the one hand the first and second upper and first and third lower rows of teeth and on the other the upper beak (Compare Charts 4, 7, and 8), (2) those involving on the one hand the first and second upper and first and second lower rows and on the other hand the third lower row of teeth, (3) those involving on the one hand the first and second upper rows of teeth and on the other hand the average of the right and left parts of the second upper row, and (4) that of the second upper row and its median space. The ratios of the other combinations, though individually less distinctive, may in some instances prove to be the deciding character "in favor of" the one or the other species. They are, then, not to be discredited.

Appreciating fully that the number of species here available for comparison is small and that species of the same genus or family would be indeed more difficult to distinguish, it is concluded that this study does indicate that tadpoles may be divided at any stage of existence when the horny teeth and beak are present into relatively small, if not specific groups, on the basis of all the ratios between the rows of teeth and between the rows of teeth and the upper beak, provided the ranges of such ratios are established for all stages of tadpoles of each species. These ratios are not established at present for all ages of tadpoles of the different species except those established in this study. But it is proposed to establish such ratios through the method here introduced to this type of study for tadpoles of all species available from definitely identified parents.

SUMMARY AND CONCLUSIONS

Growth phenomena concerning the rows of teeth in tadpoles, particularly of *Bufo fowleri*, may be summarized briefly. The oral disc increases in size by extension of its radii; these "extensions" may be irregular or disproportionate; and the radii may extend from more than one center of growth. The extension of these radii forces the rows of teeth peripherally, also forcing an increase in length. This obligatory increase in length is brought about by divisions of cells in a plane parallel to the radii of the disc and at right angles to the surface of the disc. These cell divisions ultimately result in divisions of teeth. The rows of teeth also increase in length by addition of tooth-forming cells at their ends, resulting in a circumferential extension of the disc by growth of the rows at either end. The disproportionate extension of the radii of the disc, and the extension of the rows of teeth further around the circumferences, of which they are arcs, result in a changing degree of curvature of the rows of teeth. However, those rows of teeth growing in length more

rapidly also increase in arc length/chord length ratio more rapidly, thus making comparisons between chord lengths of rows more nearly constant than comparisons between arc lengths of the same rows.

Arc length of a row of teeth compared with total body length of a tadpole affords the best expression of relative growth of a row of teeth until near the onset of the metamorphic climax. However, chord length of a row of teeth as compared with body (only) length of a tadpole affords a very satisfactory standard for comparison of the different rows of teeth. From examination of such relative growth rates and of percentage increases in length, it has been seen that all rows of teeth and the upper beak have their rates of growth similarly affected by the various conditions of growth, and change growth rates simultaneously and in a similar manner, though possibly to a different extent. In this connection it should also be pointed out that increase in length of a row of teeth is independent of the original length of the row, and that increase in length is not a constant fraction of the entire growth complex of the row.

Since growth rates of the rows of teeth are similarly affected by conditions of growth, and since arc length/chord length ratio increases somewhat in proportion to percentage increase in length of a row, it may be concluded that chord lengths of rows of teeth do bear some constant relation to each other and that the use of such relations between rows of teeth and between rows of teeth and the upper beak as taxonomic characters may be justified from the viewpoint of having an explainable basis. It may be further concluded that chord lengths of the rows of teeth and the upper beak are the more frequently comparable measurements.

It should also be pointed out that, since increases in lengths of the rows of teeth are not proportionate to their original lengths, the relationship between the rows of teeth may change. Thus, the combinations of rows of teeth affording ratios more nearly constant for all ages are the rows of more nearly equal lengths. However, ratios of such combinations of rows of teeth are less distinctive of a given species.

Aside from (1) showing that growth phenomena of the oral disc offer an explainable basis for the use as taxonomic characters of ratios between the various rows of teeth and between rows of teeth and the upper beak and (2) showing that the relative constancy of the ratios of the chord lengths of such various different combinations may be determined from a study of these growth phenomena as well as from actual comparison of the different ratios, the results of the present study have some practical application.

Obviously, distinction of a given species can rarely be reliably made on the basis of the ratio afforded by a single combination of rows of teeth. However, if the results from the study of the three species herein

concerned may be taken as an indication, it is believed that on the basis of the ratios of all the possible combinations of rows and upper beak tadpoles of all ages may be separated into small, if not specific, groups.

The combinations affording ratios (between chord lengths) more constantly distinctive between the tadpoles of the three species studied (*Bufo fowleri*, *Pseudacris nigrita triseriata*, and *Rana pipiens*), are (1) those involving on the one hand the various rows of teeth and on the other hand the upper beak, (2) those involving on the one hand first and second upper and first and second lower rows of teeth and on the other hand the third lower row of teeth, (3) those involving on the one hand the various complete rows of teeth and on the other hand the average of the right and left parts of the second upper row.

The combinations affording ratios (between chord lengths) that are less variable with change in age of the tadpoles are (1) those involving the first and second upper and first and second lower rows of teeth, and (2) those involving on the one hand the various rows of teeth and on the other hand the upper beak.

The "graphic" method employed for determining and studying the ratios is a very satisfactory method for such study, since it eliminates endless calculations and shows in a compact and readily interpretable manner the course of ratios of a given combination of rows of teeth throughout all ages of tadpoles. The method also has further applications that cannot yet be made. When the ratios of all combinations of rows of teeth and of rows of teeth and upper beak for tadpoles of all ages or sizes of several species are known, "graphic keys" may be made which will eliminate the necessity of calculating the ratios of rows of teeth of a tadpole to be identified. By drawing on graph paper "lines of equal proportions" to represent the limits of the ratios of the combination of rows in question for different species, and by using such a graph for each possible combination such a "graphic key" may be made. By using the chord lengths of the rows of teeth and of the upper beak as coördinates in all possible combinations the points determined by the various pairs of coördinates will fall within limits (on the different graphs) peculiar to certain species. Although a given range of ratio may be common to several species, it is not likely that the ranges of the ratios of the different combinations would be common to the same group of species in each instance.

As to similarities in growth phenomena, in ratings as to constancy of ratios of the different combinations of rows of teeth, etc., and in actual ratios of the combinations of rows of teeth, etc., there appear to be different correlations between certain of the three species of tadpoles studied. *Bufo fowleri* and *Pseudacris nigrita triseriata* are more nearly similar according to the above-mentioned particulars than are either *Bufo fowleri*

and *Rana pipiens* or *Rana pipiens* and *Pseudacris nigrita triseriata*. Although the advisability of attributing systematic significance to any larval character is doubtful, it is of note that the relations as indicated by this study of the larval mouth apparatus coincide with the relations generally conceded to exist between adults of the species.

As to the ratios of combinations of rows of teeth, etc., as given by Wright (1929) for the species involved in this study, the following conclusions may be drawn. (1) The ranges of ratios as given are not of sufficient extent to include ratios in younger tadpoles. (2) The ranges of ratios as given for *B. fowleri* are not of sufficient extent to include ratios of a "normal" percentage of "mature" tadpoles. Also, it has been shown in this study that the description, as given by Wright and Wright (1933), of tadpoles of *Pseudacris nigrita triseriata* as having only two lower rows of teeth is erroneous. Tadpoles from mated pairs known to be *Pseudacris nigrita triseriata* (identification by Dr. G. K. Noble) have the third lower row of teeth added after attaining a body length of from 2.91 to 3.57 mm. There are two possible explanations of the error. (1) There may be a geographical variation in tadpoles of the species. (2) The description may have been made from incorrectly identified tadpoles.

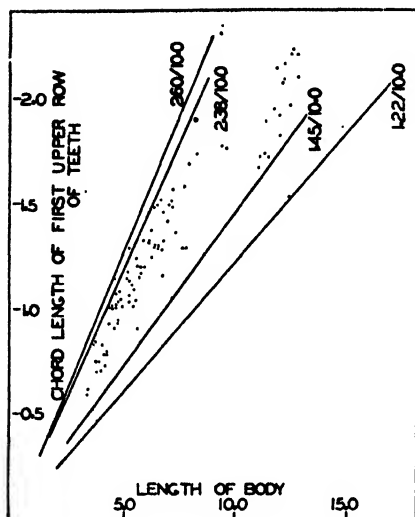
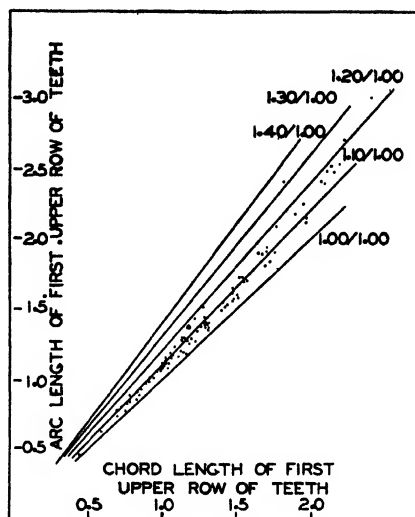
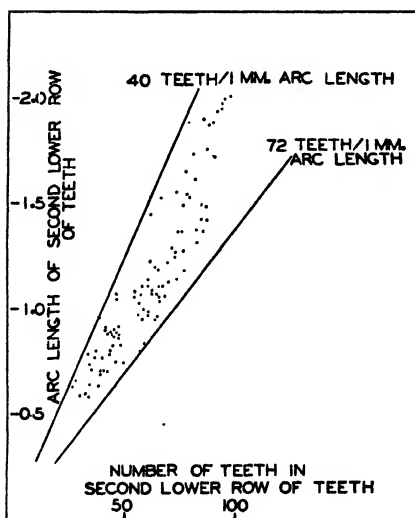
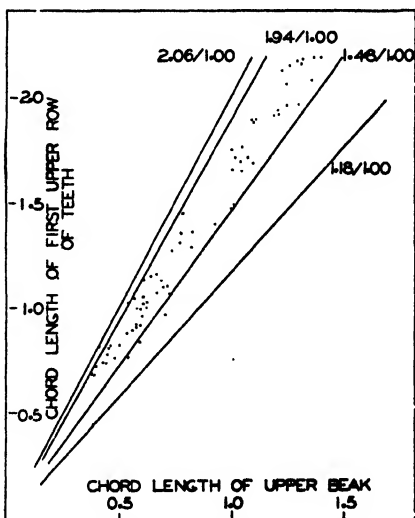
CHARTS

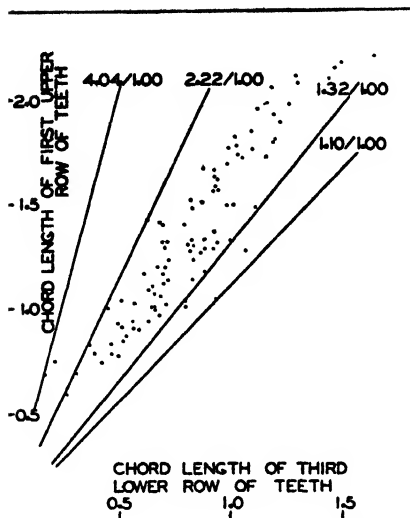
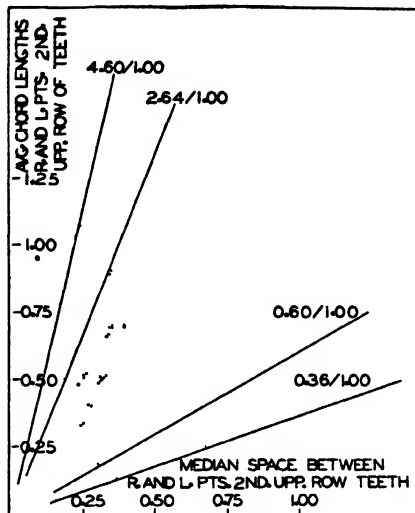
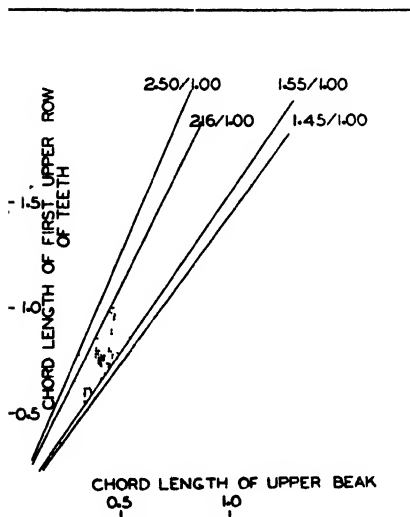
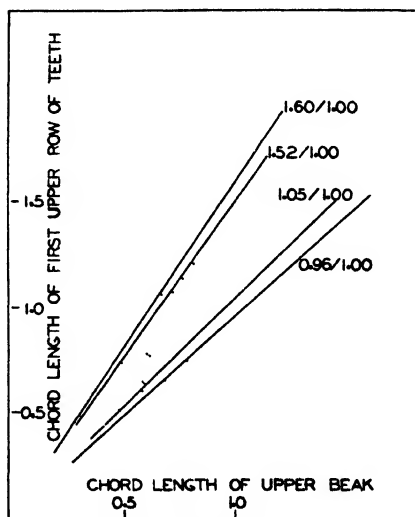
The data in the tables in the text were gathered from charts similar to those on the following pages. Since it was impracticable to publish the complete set of charts and thus duplicate the data in the tables, eight representative charts have been included as illustrative of the method used.

The charts for the most part serve the purpose of showing ratios between various sets of measurements plotted as coordinates. Each plotted point represents the ratio in a single animal of the two measurements plotted.

The lines on the charts, since each line passes through zero, are lines of equal proportions, the proportion represented by each line being indicated thus: 1.22/1.00, 1.45/1.00, etc. These lines have been drawn so as to include all points and thus represent upper and lower limits of the ratios of the two measurements in question. Lines have also been drawn to exclude extreme ratios (never more than 5-6%).

The numbers giving the values of coordinates are in each case millimeters, with the exception of the values of the abscissas of Chart 3, where they represent numbers of teeth.

CHART 1.—*Bufo fowleri*CHART 2.—*Bufo fowleri*CHART 3.—*Bufo fowleri*CHART 4.—*Bufo fowleri*

CHART 5—*Bufo fowleri*CHART 6—*Bufo fowleri*CHART 7—*Pseudacris nigrita triseriata*CHART 8—*Rana pipiens*

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